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El lepidóptero satúrnido representado en la cubierta es la *Graellsia isabellae* (Graells) de los pinares del centro de España; × 1/3.

(Dibujo de S. Martínez.)

# Una nueva especie del género *Ariasella* Gil, con breves consideraciones sobre la reducción del tórax en los Taquidrominos ápteros

## (Dipt. Emp.)

POR

J. Gil Collado.

(Lám. II.)

En una reciente excursión a Picos de Europa, mi querido amigo y maestro el Prof. Bolívar y Pieltain encontró un ejemplar de este género que pertenece a una nueva especie, que me complazco en dedicarle por el interés que ha demostrado por dicho grupo de Dípteros ápteros o braquípteros, cuyos tipos han sido siempre capturados por él.

Este hallazgo me ha deparado una ocasión para comparar los escleritos torácicos que integran el tórax en dicho género, así como en *Pieltainia*, con el de una especie de *Tachydromyia* (*T. calceana*), que muestra analogías indudables con ambos.

De dicho estudio comparativo se deducen algunas consideraciones que he creído oportuno unir a la descripción de la citada especie, y que espero ampliar cuando una mayor riqueza de material y de especies conocidas con diversos grados de apterismo me permitan realizar un trabajo más profundo sobre dicho fenómeno en las distintas formas de la subfamilia.

### **Ariasella pieltaini** nov. sp.

(Lám. II, fig. 1)

Tipo: ♀ de la Porra de Enol, VIII-1935 (C. Bolívar).

Coloración: cabeza negra brillante; antenas amarillentas, con arista más oscura; palpos amarillentos. Tórax negro brillante, como pulimentado. Patas ocre-amarillentas, con las caderas II y III, así como el extremo de los trocánteres y el último artejo de los tarsos, más oscu-

*

ros, sobre todo estos últimos. Alas parduscas, con su extremo negruzco. Abdomen pardo-negruzco también muy brillante. Cercos oscuros.

Cabeza globosa, con su borde anterior hemisférico y el postero-inferior casi recto y formando un ángulo entrante cerca de su extremo. Frente muy estrecha, reduciéndose aún más hacia las antenas; ocelos como en *A. semiaptera* (lám. II, fig. 2). Cerdas ocelares más robustas y las occipitales más numerosas y grandes que en ella. Antenas de igual forma que en dicha especie; artejo 1.° muy corto, no visible en perfil; 2.° subcilíndrico y 3.° oval corto, con la arista, de igual longitud que la cabeza, implantada en su borde dorsal antes del extremo. Palpos cilíndricos, algo más finos que en aquélla y alcanzando dos tercios de la longitud de la trompa; en su extremo llevan una fuerte cerda ante-

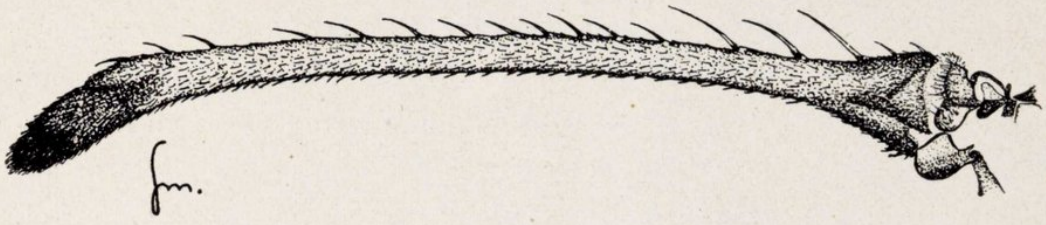


Fig. 1.—Ala de *Ariasella pieltaini* nov. sp. ♀.

rior y otra posterior más débil. Trompa de igual forma. Ojos reniformes, cóncavos posteriormente, si bien quizá algo menos que en ella.

Tórax con los escleritos casi iguales a los de *A. semiaptera;* pero el mesonoto es ligeramente más giboso, impidiendo el brillo distinguir bien las suturas de unión de los distintos escleritos. Prácticamente, el tórax es lampiño. Su dimensión con respecto a la cabeza es poco menor que en dicha especie. Patas de forma y proporciones parecidas, pero cubiertas de pubescencia más densa y negra, que contrasta con el color pálido del tegumento.

Alas (fig. 1), alcanzando hasta el extremo del primer terguito visible, compuestas de un tallo ligeramente encorvado y terminado en un ensanchamiento algo curvo y marcadamente más oscuro. En ellas no puede verse venación de ninguna clase. El borde anterior o costal lleva una serie de cerdas que representan las cerdas costales, que, debido a la reducción alar, aparecen marcadamente más grandes. Escámulas bien marcadas, así como los escleritos axilares que se ven en la figura.

Abdomen muy distendido en nuestro ejemplar, desprovisto de pubescencia visible. Cercos ligeramente más finos que en *semiaptera* y casi cilíndricos.

Long., 2,9 mm.

Loc.: Asturias: Porra de Enol, sobre Covadonga, a 1.250 m. de altura, 1 ♀ tipo.

Observaciones.—Se distingue esta especie de *semiaptera* por caracteres perfectamente definidos.

Fig. 2.—Ala de *Ariasella semiaptera* Gil ♀.

Dejando aparte su talla mayor, tenemos en primer lugar la forma de las alas, que en la citada especie aparecen, como lo indica la figura 2, escuamiformes, mientras en ésta son largas y en forma de tallo. La proporción del tórax y la cabeza, como ya hemos indicado, es algo distinta. La coloración de las patas es diversa, y la pubescencia es más abundante en *pieltaini*.

## La reducción del tórax en los géneros *Ariasella* y *Pieltainia*.

Para la mejor comprensión de la estructura del tórax en estos Empidos he creído conveniente compararla con la de los géneros próximos. Es indudable que el que muestra mayores analogías con los dos antedichos es *Tachydromyia*, cuyos caracteres denotan una íntima relación, tanto en la forma de la cabeza como en el aguzamiento anterior del tórax, proporciones de las patas, etc.

En dicho género (fig. 3) el tórax aparece marcadamente contraído en su parte anterior, y posee las callosidades humerales muy desarrolladas, que dejan una estrecha banda del mesonoto entre ellas. La división entre el preescudo y el escudo mesotorácicos no es marcada, por cuanto la sutura transversa no existe o, a lo sumo, está sólo esbozada. El escudete es moderadamente grande, semicircular, y el postescudete, convexo, es bastante largo, apareciendo por detrás de él una estrecha faja que debe de representar el terguito metatorácico, cuya distinción del epímero correspondiente no está clara. En conjunto, el tórax es muy abombado hacia el medio del mesonoto.

El antepronoto es estrecho y aparece como un anillo incompleto a un nivel mucho más bajo que el del mesonoto. El postpronoto o callosidades humerales está sumamente desarrollado.

Lateralmente la propleura aparece como una pieza única, en la que no se puede distinguir el episternón del epímero, estando separado por una pequeña sutura, casi indistinta del pronoto posterior. El anepisternón y el esternopleurito mesotorácicos aparecen también soldados en un solo esclerito muy grande, en el que no he podido observar restos de sutura, si bien es difícilmente visible por su brillo muy intenso. El pteropleurito es muy estrecho comparativamente al de *Rhamphomyia*, siendo el meropleurito, por el contrario, mucho más

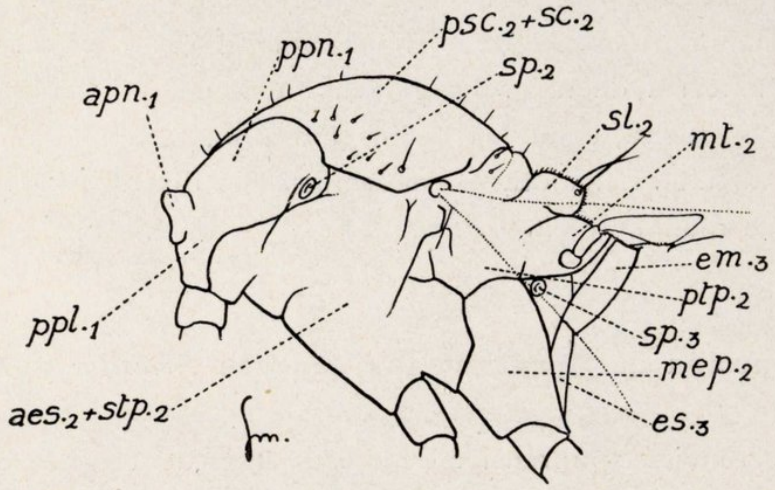



Fig. 3.—Tórax de *Tachydromyia calceana* Meig.

grande. Por lo que respecta al metatórax, el epímero aparece muy débilmente quitinizado en su mitad inferior, y por ello termina lejos de la cadera III, separado de ellas por el episternón, que es triangular, muy estrecho y largo.

El tórax de *Ariasella* (fig. 4), que es indudablemente más primitivo que *Pieltainia*, presenta dorsalmente un desarrollo mucho mayor del pronoto posterior o callosidades humerales, que casi confluyen en su parte anterior, como se ve en la figura, extendiéndose hasta alcanzar casi la tercera parte de la longitud del tórax y la mitad de la del mesonoto, excluído el postescudete. En conjunto el mesonoto es mucho menos convexo; el preescudo y el escudo están fundidos en una sola pieza por falta de la sutura escutal, como en *Tachydromyia;* la anchura del terguito está disminuída por avanzar la sutura pleural hacia

arriba. El escudete se ha reducido, carácter ya indicado por Bezzi en los Dípteros ápteros, no solamente por su menor tamaño, sino por ser menos prominente, como puede apreciarse en el dibujo. El postescudete es moderadamente ancho y desde luego algo menor que en el último género. Detrás de él aparece el terguito metatorácico muy estrecho, continuado por detrás por un esclerito medio alargado y estrecho, separado por unas finas suturas de las piezas pleurales, que puede representar, a nuestro juicio, la parte de escudo metatorácico, siendo la anterior el preescudo. Lateralmente puede apreciarse la soldadura del pronoto anterior con el resto del protórax, del que está separado por una sutura incompleta; no se distinguen suturas que delimiten el episternito del pronoto posterior. El esternopleurito no está bien delimitado del anepisternón, como en aquél, siendo sus proporciones casi idénticas. Por el contrario, el pteropleurito, y sobre todo el meropleurito, se han hecho mucho más estrechos, aunque continúan bien separados. El metatórax ha aumentado considerablemente de tamaño, siendo la base del episternón mayor que su altura, y el epímero muy amplio y bien quitinizado llega a ponerse en contacto con la cadera III. En ambos sexos las proporciones de los distintos escleritos son iguales.

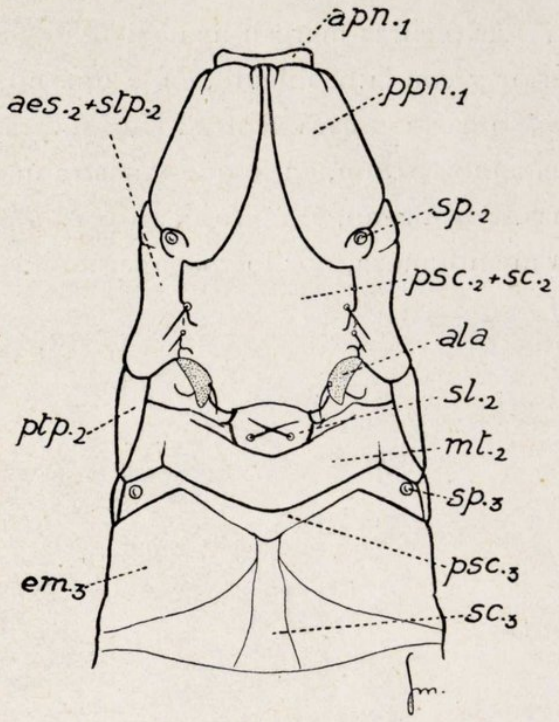


Fig. 4.—Tórax de *Ariasella semiaptera* Gil.

En el tórax de *Pieltainia* (fig. 5) se ha realizado un simplificación mayor, siendo las suturas notopleurales indistintas; el pronoto, sin embargo, parece ser algo menor que en aquélla, por lo cual se aproxima más a *Tachypeza*, a cuyo género es indudablemente másafín.

El escudete es más pronunciado que en *Ariasella* y más promi-

nente. El postescudete está quizá algo más desarrollado, mientras el terguito metatorácico es moderadamente estrecho y no diferenciado del metepímero.

Las pleuras marcan una soldadura del pronoto anterior con el posterior y con la propleura, en la que no existen suturas marcadas, llegando hasta la cara ventral. Una sutura fina separa el esternopleurito del anepisternón, en lo que muestra una diferencia con las otras formas. Por último, el meropleurito es amplio, aunque su parte inferior es membranosa, por lo cual aparentemente no llega hasta la cadera III,

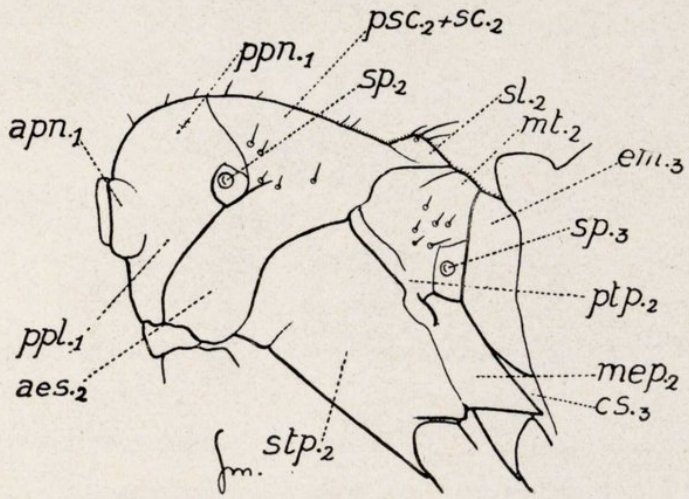



Fig. 5.—Tórax de *Pieltainia iberica* Arias.

y el episternón metatorácico se extiende hasta ponerse en contacto por encima con el pteropleurito.

Ahora bien; de estos datos parece deducirse bien una atrofia del mesotórax en ambos géneros con alas atrofiadas, compensada en parte por un desarrollo mayor de los otros dos segmentos, bien que éstos hayan conservado sus proporciones primitivas, pero al reducirse el mesotórax el conjunto del tórax resulte más pequeño, por lo cual aquéllos aparentemente estén hipertrofiados. El único modo de comprobar lo que ha ocurrido con estos escleritos es su comparación con piezas del exosqueleto que no hayan debido ser afectadas por la atrofia alar. Desde luego debe desecharse, a nuestro juicio, la comparación con el abdomen, que por su mayor o menor distensión puede arrojar cifras muy variables, por lo cual hemos elegido, bien el fémur anterior, bien la cabeza, expresando los resultados en el cuadro adjunto.

Aunque estas cifras están obtenidas sobre un escaso número de ejemplares, tienen el valor innegable de su gradación casi perfecta.

| INDICE | *Tachydromyia calceana* Mg. | *Ariasella semiaptera* Gil. | *Ariasella pieltaini* Gil. | *Pieltainia iberica* Ar. |
|---|---|---|---|---|
| Long. cabeza / long. fémur I. | 0,56 | 0,59 | 0,57 | 0,75 |
| Long. tórax / long. fémur I. | 1,1 | 1,0 | 0,95 | 1,0 |
| Long. fémur III / long. fémur I. | 1,5 | 1,7 | 1,7 | 1,7 |
| Long. tórax / long. cabeza. | 2,0 | 1,7 | 1,6 | 1,4 |
| Long. fémur III / long. cabeza. | 2,7 | 2,8 | 2,1 | 2,0 |

Estudiando los diversos índices, si se toma como unidad el fémur I, observamos que sus proporciones, comparativamente al tórax, quedan casi invariables; en cambio, si se las compara con las cefálicas son marcadamente distintas en las diversas formas, sobre todo en *Pieltainia*, en la que aparece notablemente reducido.

La proporción entre los fémures I y III varía ligeramente en las formas ápteras en comparación con *T. calceana*, pero permanece invariable entre aquéllas.

Si en lugar de elegir el fémur I tomamos la cabeza para nuestro objeto, podemos apreciar una gradación comparativamente al tórax, a partir de *T. calceana* hasta *Pieltainia*, en la cual aquélla aparece notablemente mayor. No acontece lo mismo comparando la cabeza con los fémures III ni con los I, como hemos dicho anteriormente.

Con respecto a la morfología comparada de los escleritos torácicos en dichos tres géneros, se deducen de ella una serie de consideraciones acerca de las modificaciones a que el apterismo da lugar.

En primer término, se marca una notable disminución de convexidad del tórax, originada por el aplanamiento del mesonoto, a consecuencia de la atrofia de los músculos del vuelo, acusada en perfil, en el que se muestra casi plano, y acentuada cuando se le ve por encima, porque las suturas notopleurales, cuando se muestran aparentes, avanzan

considerablemente hacia la región mediana, estrechando bastante el esclerito antedicho.

También se marca la atrofia del mesotórax comparativamente a los otros dos segmentos, que aparecen notablemente ampliados. El pronoto posterior se hace más grande, pero al mismo tiempo más aplanado y no tan prominente, borrándose la separación entre él y el resto del protórax. Mientras en *Ariasella* las suturas notopleurales están bien marcadas, desaparecen en *Pieltainia,* lo cual, a nuestro juicio, representa una mayor especialización en el sentido del apterismo.

El escudete, como ya lo había hecho resaltar Bezzi, muestra una reducción bien visible, y lo mismo ocurre con el meropleurito, aunque en dicha pieza parece no debe de jugar un gran papel la atrofia de los órganos del vuelo.

Por el contrario, el metepímero experimenta un mayor desarrollo, no sólo relativo, sino también absoluto, a nuestro parecer, ya que, incluso cuando se le compara con el pronoto posterior, aparece agrandado. Quizá esté relacionado este fenómeno con la hipertrofia de los músculos de las patas, observada por Mercier en las formas ápteras, ya que el tercer par es el más largo, aunque no el más robusto.

Un detalle interesante lo acusan las escámulas. En los géneros de la subfamilia muestran éstas una reducción que parece debiera acentuarse en las formas semiápteras, ocasionando su completa desaparición. Por el contrario, como se ve bien en las dos figuras, no sucede así, sino que siguen bien aparentes e incluso no han experimentado una disminución tan grande como la de los órganos del vuelo.

En lo que respecta a las patas, Bezzi ha afirmado que en las formas ápteras sufren una hipertrofia, haciéndose más robustas que en las formas normales aladas. Sin embargo, de nuestro estudio se desprende que, lejos de ser así, se reducen proporcionalmente al tórax, y aunque los fémures posteriores varían en su relación con los del primer par, no por eso se muestran más robustos, para darnos lugar a pensar, como indica dicho autor, una adaptación al salto en los Dípteros ápteros, sino que continúan delgados.

El dimorfismo sexual referente a las alas, citado por varios autores y que se presenta muchas veces en la naturaleza, se muestra sobre todo acusado en *A. semiaptera;* pero, en cambio, nos inclinamos a creer que el macho de *A. pieltaini* debe asemejarse bastante más a la

hembra en este respecto, por presentar sus alas un desarrollo comparable al de aquélla, si bien hasta no poseer dicho sexo no puede afirmarse en concreto. Nos basamos para nuestra suposición en la analogía de proporciones torácicas en ambos sexos y a que en esta especie la cabeza presenta las mismas proporciones con respecto al tórax, lo que indica un grado de apterismo parecido, pero no menor.

Respecto a la causa de la atrofia alar en los Dípteros, es indudable que ha de ser muy distinta en los diversos grupos; pero refiriéndonos al de los Taquidrominos, queda, a nuestro juicio, bastante oscura.

Podría aducirse la influencia de su habitat eminentemente pratícola y, por lo tanto, poco favorable para el vuelo, pretendiendo encontrarle una explicación lamarckiana. En este sentido la frecuencia de las formas ápteras entre los dípteros que viven en las praderas, y la relativa abundancia de casos de reducción alar en la subfamilia, además de la especial estructura del tórax en algunas de las formas aladas, parece proporcionar apoyo a dicha hipótesis; pero de todos son conocidas las objeciones que esta teoría ha suscitado, y que la hacen inaceptable.

Tampoco nos parece satisfactoria la hipótesis mantenida por Dewitz de la exposición de la larva y de la pupa a temperaturas y condiciones climáticas extremas, con la consecuencia de una inhibición del desarrollo de los histoblastos y de las alas, a pesar de que apelando a dichos procedimientos y a medios químicos consiguiese tener adultos ápteros, pues, como ya hace constar Keilin, éstos son sumamente defectuosos. En el caso de *Ariasella* y *Pieltainia*, lo mismo existen en las zonas montañosas que en las llanuras de poca altura sobre el nivel del mar, a condición de que haya césped abundante y denso y humedad considerable que permita la vida a los pequeños Sciáridos, que el Sr. Bolívar ha podido apreciar que son presa frecuente de estos dípteros.

Bezzi se inclina a creer que este fenómeno se debe a causas internas o determinadas, en relación con la teoría de la hologénesis. Cuénot y Mercier observan que la atrofia alar de los Pupíparos no está en relación con la muscular y que en realidad la desaparición de los músculos vibratorios del vuelo parece acontecer por variaciones bruscas en el número de sus fibras, por causa primordial desconocida, lo que ocasiona un menor uso de las alas, que conduce a su desaparición.

La atrofia alar originada como mutación aparece con su máxima claridad en *Drosophila,* y, según Mercier, es debida a idéntica causa la que presenta *Striphosoma sabulosum;* pero, sin embargo, en ambos está desligado dicho fenómeno de la atrofia de los músculos del vuelo, puesto que en ambas especies se encuentran éstos perfectamente desarrollados, mientras que en los Taquidrominos que nos ocupan parece que la reducción del mesotórax y el aplanamiento del mesonoto sean signos evidentes de que los músculos vibratorios han experimentado una atrofia.

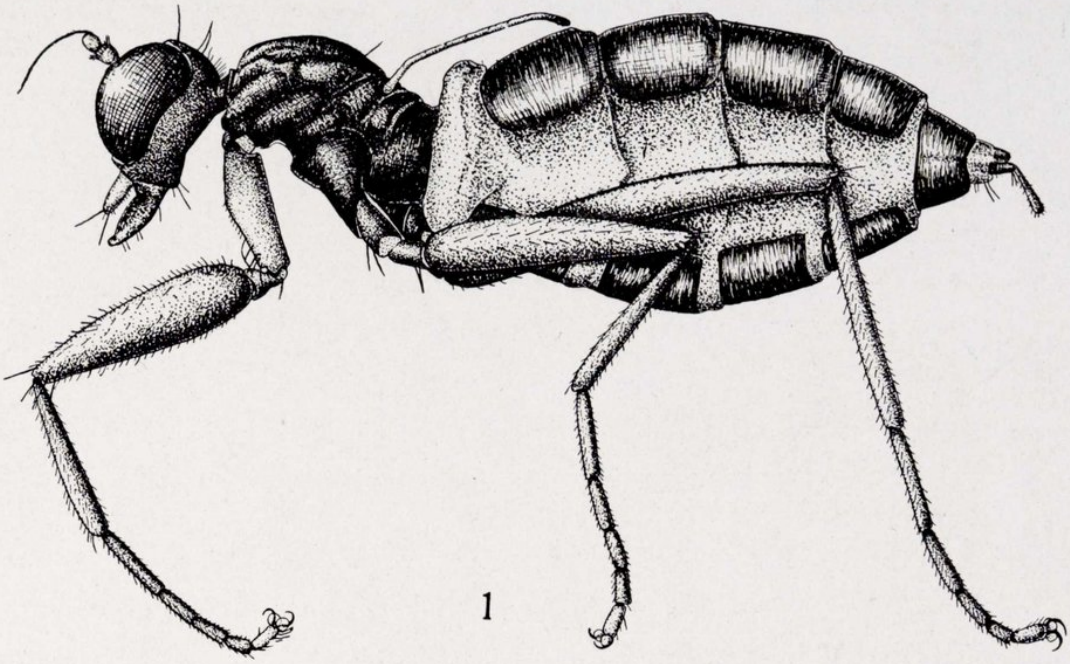
Sin embargo, no tengo noticia de que se hayan estudiado los efectos que esta atrofia alar haya podido causar en generaciones sucesivas de la primera.

A mi juicio, es muy probable que la causa del apterismo de estos Taquidrominos sea debida a una mutación que al perpetuarse en las generaciones sucesivas ha dado origen a la atrofia de los músculos vibratorios, con todas sus consecuencias de cambio de forma del tórax, desproporción entre la cabeza y el mismo, modificaciones de las suturas torácicas, etc.

A este respecto creemos sumamente interesantes las observaciones de Mercier acerca de la desaparición de los músculos vibratorios después de la pérdida de las alas en *Carnus hemipterus* y en *Lipoptena cervi,* que cree debida a cambios profundos en el metabolismo de dichos dípteros a consecuencia de la hematofagia y de la temperatura constante.

## Explicación de la lámina II.

Fig. 1.—*Ariasella pieltaini* nov. sp., ♀ tipo; × 30.
Fig. 2.—*Ariasella semiaptera* Gil, ♀; × 40.



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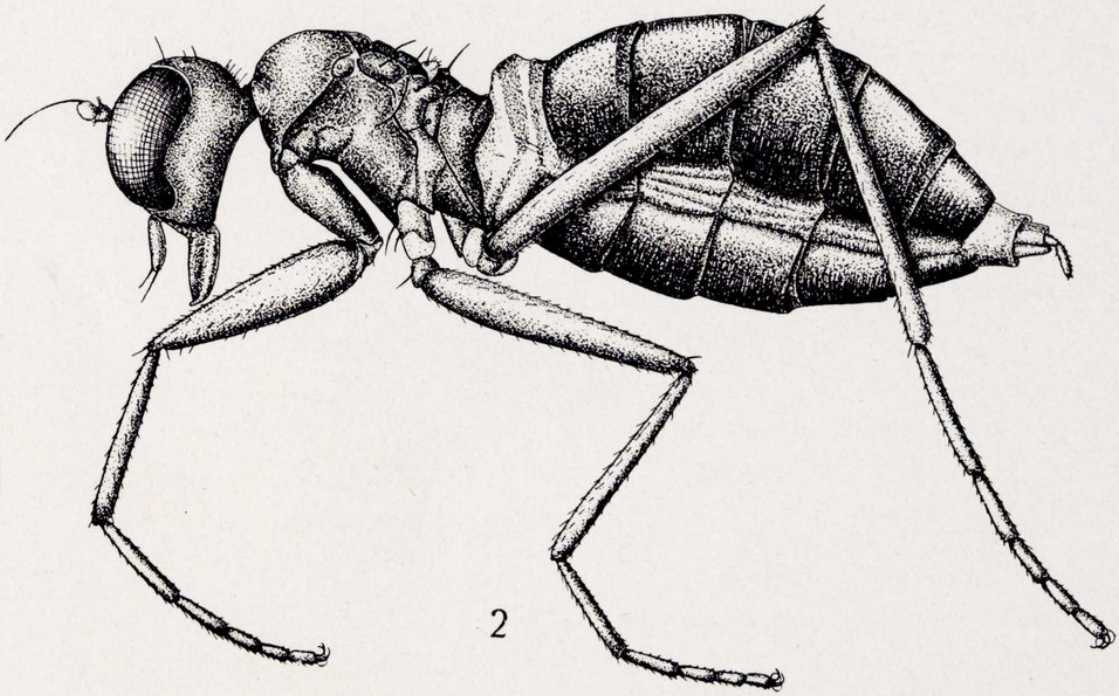

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J. GIL COLLADO: Una nueva especie del género *Ariasella* Gil, con breves consideraciones sobre la reducción del tórax en los Taquidrominos ápteros.

# The nesting habits of solitary bees

## A comparative study

BY

S. I. MALYSHEV.

Entomological Laboratory,
University of Leningrad.

(Láms. III-XV.)

«Cette histoire n'a pas encore, que je sache, été méthodiquement entreprise. Il est à souhaiter qu'elle le soit, car elle toucherait à plus d'un problème aussi grand que ceux de bien des histoires humaines.»

M. MAETERLINCK: *La vie des abeilles.*

## Preface.

This treatise presents the general part of my special studies on the ethology of various solitary bees. At the present time many of these investigations have already been published in different periodicals, and others yet wait their turn (see below the index of the author's works).

A great delay, however, arose with the publication of the general part. At first it was written in Russian, but in the year 1927 the Russian manuscript was put into English. Unfortunately the translation proved to be unsatisfactory, and I take the opportunity to express my grateful acknowledgments to Mr. O. W. Richards of London for his great work in revising my English text, which he has done only in the interest of Science. I shall be very glad, if his kind assistance is appreciated by all those, who find my work a contribution

to the progress of our knowledge of the habits and behavior of Insects.

Besides I have also a pleasure to express my cordial thanks to Dr. B. P. Uvarov and Prof. F. Balfour-Browne for their kind and succesful cooperation in this matter.

The third part of the complete treatise dealing with the origin and evolution of instints in *Hymenoptera* is not revised yet, but the author hopes, that it will be published in a not distant future.

## Introduction.

The bees (*Apoidea, Anthophila*) together with various wasps and the ants form, as is known, the large group of stinging hymenoptera *(Hymenoptera aculeata)*. The larvae of all bees and wasps, unlike those of ants, develop in definite, nearly always strictly limited compartments, isolated from one another, termed cells. The moving to and fro of the eggs and developing larvae, so characteristic of the life of ants, is not practised by wasps and bees; in whatever cell the egg of a wasp or bee is laid, there, in the normal course of events, development right up to the adult insect takes place.

Apart, however, from this similarity between wasps and bees, there is an essential biological difference: wasps nearly always feed their larvae on animal food: insects of different orders and stages, and spiders *(Araneina)*. The bee-larvae, on the contrary, are exclusively or mainly vegetarian, the mother feeding them on a mixture of nectar and flower pollen, sometimes mixing with it to a varying extent the secretions of her salivary glands. Only exceptionally «royal jelly» is secreted into the cell and entirely replaces pollen and honey.

The bee family (or superfamily) falls into three groups from the biological point of view, according to the mode of life adopted: viz., solitary, social and parasitic bees.

Solitary bees build their nests and provide them with all that is necessary independently, without help from other members of the species. There exists, therefore, among them neither distinct castes nor division of labour and if the latter is sometimes observed, it occurs

only casually and manifests itself moreover under very primitive forms. They never appear to store up provisions in special receptacles devoted to that purpose only (storage cells). They build their cells and provision them one after the other, consecutively.

Social bees, at least in the typical and most common cases and when conditions are favourable, live in communities, the members of which stand in close relationship to each other. The activity of the individual members of such a community is directed almost entirely to the securing of the welfare of the whole. To attain this end in bee-communities a separate caste of auxiliary females (sexually underdeveloped) or workers (underdeveloped females with their structure adapted to their work) has been evolved in addition to the sexually developed females (of which there is usually only one) and the males. As far as we know, all social bees store up provisions in their nests, both for the growing young and for their own use, in special receptacles (storage cells). They build cells and provision them in series, making more than one at a time and employ a material secreted by special cutaneous glands (wax glands); their architecture and method of nest-construction always belongs to the type of so-called free or independent nests.

Parasitic bees, or cuckoo-bees, as they are also called, do not build nests themselves, and store no provisions, but lay their eggs in cells of other species of solitary or social bees, where, accordingly, their larvae are fed at the expense of others. When adult only sexually developed females and males are represented.

As regards a morphological basis for dividing the bees into three groups, systematists are unable to indicate characters which will refer a bee in every case to the correct group. Thus even so peculiar a structure as the presence of a «basket» (corbicula) on the tibiae of the hind legs, a structure common to all social bees, is not confined to them but occurs occasionally in solitary bees (*Euglossa, Canephorula*). It may be noted, however, that any bee in which some individuals have underdeveloped ovaries and collect provisions for the nest, is invariably a social species. Solitary bees are easily distinguished superficially from the cuckoo-bees which live at their expense, the latter being usually without the dense hairy coat normally characteristic of the former; the parasites, further, lack the special apparatus

for collecting the pollen of flowers and moreover are often brightly coloured. The long controversy as to the systematic position of the genus *Sphecodes* and some other genera may be mentioned—without referring to a variety of other exceptions—as showing that the structural basis of classification is at present insufficient. Various attempts at finding a new morphological definition of the parasites have indeed been made. Thus Cockerell and Emerson (1902) found that industrious solitary bees always have a comb of bristles on the lower side of the mandibles, a structure which is wanting in the cuckoo-bees, which have only a row of short hairs in this position. I am not prepared to say to what extent this character will be considered sufficient and workable.

At any rate the morphological characters used by systematists divide the bees into groups cutting right across the biological classification, though even here authorities are by no means unanimous as to what groups shall be adopted [1]. The division of the bees into lesser units, is, too, not yet completed and the description of new genera and species continues actively.

Bees occur in all parts of the world and are distributed from the arctic circle in the north to the southern extremity of the earth (Tierra del Fuego, Tasmania) and from dunes near the sea-shore up to high levels in the Alps and even in the Pamir and the Himalayas (2.000-4.000 m.). As they approach the cold polar region the number of species and individuals rapidly decreases. Thus on the islands of the Arctic ocean (Novaya Semlya, Vaigatch, Iceland), on the peninsulas of Alaska, Labrador, Northcape and even the Murman coast, only humble-bees, leading a semi-solitary life, are found and on Spitzbergen even these are wanting. In the Antipodes also a humble-bee (the Chilian *Bombus dahlbomi* Guérin) and certain species of *Halictus* penetrate farthest southwards.

Besides temperature, humidity also has doubtless a great influence on the geographical distribution of bees. Even in warm, and hot countries if they have a frequent and heavy rainfall the number of species and individuals of bees is comparatively very small, and this is even more marked in cold lands. This is especially the case in

[1] Compare Sharp, 1902; Ashmead, 1899; Robertson, 1904; Börner, 1919; Friese, 1922.

the damp primeval forest along the Amazons and in the Archipelago of the Sunda Isles. I was able to convince myself that this was true also of the bee fauna near Batum during the months of June and July 1914. The influence of excessive humidity appears to tell here mainly in an indirect way by the influence of the vegetation. The rank growth, particularly of trees and cryptogams (ferns), throwing a dense shade over the soil and the general scarcity of flowers, are here the most important factors. But there is no doubt that the actual properties of the provision stored up by the bees (particularly the hygroscopic nature of the honey) are also of great importance. It is doubtless significant that the bees living where excessive humidity is one of the main features of their environment, nest in a substratum which safeguards them against its effects (*Xylocopa* and *Megachile* of tropical forests), or make cells of watertight material, as for instance, resin or the epidermis of birch (*Trachusa serratulae* Panz., *Megachile analis* Nyl.).

From this it will be clear, that the maximum development of bee life is observed in regions having a steppe or almost desert character, and, having therefore, a dry and warm, or hot, climate along with an appropriate soil. For the richness and variety of their bee-fauna Texas, Argentina, Turkestan, and the southern valleys of mountain ranges such as the Alps and Pyrenees are specially notable.

Human activities are also of an inmense influence on the bee-fauna. Unfortunately this influence is usually destructive in the case of solitary bees. So late as May or the first half of June —I refer chiefly to Central Russia— the busy activities of a multitude of various bees may be seen in flowerstrewn meadows, glades, and the gentle slopes of ravines. But a few days after the grass has been cut this charming picture entirely disappears. Evidently the cutting of the grass is an elemental catastrophy to the bees. But the ploughing of fields and their sowing with cereal crops is even more destructive of the bee-fauna, especially as regards number of species. Fortunately, along the borders of woods, between fields, along roads, and especially railway tracks, on steep slopes, waste land and similar places and as an exception on reservations —the varieties of natural vegetation remain more or less untouched and the bees take here their harvest.

At the present time the number of species of bees is estimated

(Friese, 1922) at 20.000. Of these 12.000 are already described. The great majority of the latter refers to the number of the solitary bees and only about 500 species to the social ones. Further, one half of the described species are found in the palearctic region (Europe, Asia), whose fauna has been better studied. The remaining species are distributed over the other geographical regions as follows:

Nearctic region (N. America), 2.500 species.

Neotropical region (S. America), 1.500 species.

Ethiopian region (Tropical Africa), 1.000 species.

Oriental region (India and Malayan Isles), 500 species.

Australian region (Oceania), 500 species.

Out of the total number of bee-genera, perhaps a hundred (Friese), there are only 44 in Europe. Of the latter only two genera, humblebees (*Bombus* Latr.) an the honey bees (*Apis* L.), are social, 28 are solitary and 14 are cuckoo-bees.

The activities of solitary bees, like those of most other animals, are directed on the one hand to securing the wellbeing of the individual, and on the other to the maintenance of its young.

Excepting certain phenomena of social, family and gregarious life, these two kinds of activity, which may be called individualistic and philoprogenitive respectively, are to a certain extent typical of different periods of the animal's life. This distinction is most marked in insects with a complete metamorphosis (bees, wasps, etc.), for until a definite stage (sexual maturity) is reached the animal's activities are individualistic only, while after that stage chiefly or exclusively of the second type or philoprogenitive. This latter type of activity generally speaking is undertaken in the interests of the generation immediately following, either directly or indirectly through relations with an individual of the other sex. Thus a philoprogenitive activity, in this sense, consists both of the sexual relation and of parental care. But in the solitary bees, as in so many other animals, the work is very unequally divided between the sexes: for while the whole burden of care for the young falls on the female, the male contributes his share only to the sexual life. The manifestations of maternal care, being usually distinguished by the variety and complexity of the actions involved, is what is of the greatest interest to us in the lives of solitary bees.

If now, besides the peculiarities of behaviour already mentioned, we consider certain disturbances of the normal activities, disturbances characteristic of old age, the whole life of the female solitary bee may be divided into four periods: the first period or infancy—from the moment of hatching from the egg till leaving the cells; the second or youth—from the end of the first period till the beginning of work (sexual relations usually occur in this period); the third—the adult period, when the regular work of providing for the young is accomplished; the fourth old age—from the completion of this work till death. For practical reasons we shall begin our general survey of the life-activities of solitary bees with the third period.

## I. The Adult Period: Maternal Cares of Solitary Bees.

### Choice of Nesting-site.

The solitary bees begin their care for their young by choosing a suitable place in which to build a nest, just like the social bees in founding a new community or like the majority of the solitary wasps. Amongst the latter exceptions are found in many of the spider-wasps (*Pompilidae*), in the *Scoliidae* and more rarely in the digger-wasps (e. g. *Psammophila hirsuta* Scop.), in which the mother catches her prey before making her burrow.

Following a habit, whose origin must be sought for amongst the lower wasps, perhaps even amongst more primitive forms, the young bees do not fly far away from the place where they emerged, but settle down near their parents' nests, which, indeed, are often inherited. Owing to this habit the nests are often arranged in groups, a common phenomenon in solitary bees, so that colonies in the broadest sense (pseudocolonies) and *composite*-nests may be formed (pl. XV, fig. 67). The great frequency of this type of gregariousness suggests that we are dealing here with a general cause (viz. the habit already alluded to) and not to the effects of some accidental circumstance, such as, for instance, the impossibility, owing to some local peculiarity in the soil, of nesting over a wide area. This is supposed to be the case, however, in *An-*

*thophora nigrocincta* Lep., according to Tosi (1897). More often in other species compact colonies are found on large areas where the soil both of the surface and the lower strata is uniform, e. g., the colonies of *Dasypoda plumipes* Pz. in railway tracks between the sleepers. According to Fabre, it is probable that the first impression the young bees (in the case at least of *Osmia tricornis* Latr.) receive when they fly out of the nest, plays the most important role in this respect.

Colonies of solitary bees are met with under very various conditions. They can be observed most easily in bees which nest in the ground, whether the soil is loose or compact. Under these conditions the colonies sometimes spread over several square meters and consist of many hundreds or even thousands of nests (e. g. *Andrena ovina* Klug, *Halictus cylindricus* F., *Dasypoda plumipes* Pz., *Anthophora parietina* F., etc.). More often, however, the colonies are smaller, consisting of twenty or thirty nests, or even less, e. g. *Colletes cunicularius* L. and *Macropis fulvipes* F. Sometimes, especially on hard earthen slopes and mud-plastered walls, the bees nest so close together that it is difficult to tell where one nest ends and another begins. Matters are still more complicated by the fact that the nests of a colony are usually occupied for more than one year, so that the old tunnels and cells lie close to the new ones. If such a colony is made on a sufficiently hard substratum (e. g. a mud-wall) the matter, owing to the abundance of cells and the complexity of the tunnels, becomes quite honeycombed (*Anthophora pubescens* F., *Colletes daviesanus* Sm.). Colonies of solitary bees are met with also in thatched roofs (*Megachile bombycina* Pall., *Eriades campanularum* K., etc.) and also in wooden structures of various kinds (*Xylocopa orpifex* Sm., *Lithurgus fuscipennis* Lep.). Colonies are not found when the nesting-habitat does not allow them or when the bees themselves dislike living close together. This in *Ceratina callosa* F., I found only isolated nests, each one on a separate *Verbascum*-stem; again *Andrena florea* F., which nests in hard ground, in dry weather is occasionally only able to penetrate where there are cracks in the soil. *Chalicodoma muraria* F. is an instance of another kind, for having chosen a suitable site it defends it jealously against all invaders and prolonged contests sometimes ensue.

In the actual construction of the nests there is no collaboration even in densely populated colonies; although living in close contact with the bees remain as solitary as those living in solitary nests. If the habits show any changes indubitably due to colonial life, these are of quite a secondary nature and are shown in almost abnormal activities, such as communal defence against raids, theft, robbery, etc., on which we dwell at greater length elsewhere.

Those bees which, as already mentioned, are in the habit of settling under the parental roof or in its vicinity, sometimes build composite nests which differ from the usual solitary ones. This happens when several individuals of the same species settle in one nesting-site and use it entirely or partly for the construction of their cells. Such composite nests are widely spread amongst bees and are found in various situations, e. g. on surfaces or in holes of various kinds. The nests of *Chalicodoma pyrenaica* Lep. may be particularly large; one such nest may occupy the greater part of the eaves of a roof and may take up several square metres (Fabre). The degree of coalescence of the various nests composing the composite one also varies. In *Osmia caerulescens* L. for instance, it is difficult to tell where the work of one bee ends and that of another begins (pl. XV, fig. 67); there is almost the same difficulty in the cases of *Osmia jucunda* Sm. and *Chalicodoma pyrenaica* Lep. In bees, however, which burrow in the ground (e. g. *Halictus cylindricus* F., *Augochlora humeralis* Patton), this question can usually be decided in a more simple way. The group of cells belonging to each individual is here located in a special section of the burrow, from which a passage leads to the communal tunnel which has only one opening to the outside, i. e. the entrance to the whole nest. If we observe the bees in such a nest while the cells are being provisioned, they appear to form a true community. One after another individuals come flying to the entrance laden with pollen; if the entrance is occupied they wait till it is free, but more often those at the mouth, the 'door-keepers' make way for them, retiring into the depths of the burrow, meanwhile others are flying away to their work. This is just what is seen at the entrance of a nest of a social humble bees or social wasps. The resemblance is nevertheless merely superficial. Some authors (von Butel-Reepen, Reuter) are inclined to see in this habit of waiting at the entrance a special adap-

tation to communial life. Such waiting, is however, found also in truly solitary bees, living in isolated nests where there is no question of common labour. This Friese observed *Andrena ovina* Klug waiting at the entrance of its burrow for the departure of the cuckoo-bee *Nomada lathburiana* K., which is actually parasitic on it. *Trachusa serratulae* Pz., also if a thieving neighbour has entered her nest, does not enter until the latter has left.

Usually, though not always (*Osmia coerulescens* L.), composite nests are constructed in the old nests of the parents or at least very near them. It is in this way, by using the burrow of the maternal founder, that the common entrance to the composite terrestrial nests arises (*Halictus*, etc.). It follows that all the individuals forming the population of a composite nest are closely related to one another; usually they are sisters. The use of the maternal site for the building of a composite nest must be considered as the origin from which later on the social life of bees and wasps developed. It is well-known that humble-bee colonies in the tropics (Ihring, 1903), unlike those of temporate regions, have more than one queen (i. e. are polyginous). This is very similar to the association of solitary bees in composite nests and from this point of view social bees only live in specialized composite nests. Hence the latter may be divided into social nests and those in which there are no workers, true colonies.

Although solitary bees are in the habit of nesting in the places where they were born, yet on the whole they nest in different habitats, more or less characteristic for each species. Only a comparatively few of them, the so-called 'mason-bees' (or sculptor-bees), commonly construct their nests quite in the open. These mason-bees inhabit large cavities in stones or attach their nests to the stems of plants, or live under the roofs of buildings etc., or in special cavities (*Chalicodoma, Euglossa, Osmia globicola* Stadlm., *Anthidium laterale* Latr., etc.). The vast majority of solitary bees, however, build in small holes corresponding approximately to the size of their cells. In this case the bees may either use ready made cavities — the so-called 'lodger bees', or they make their nest-cavities themselves.

The range of ready-made cavities chosen is very wide. Thus the same bee, *Osmia rufa* L., for example, may nest in the rushes of a roof, in the deserted subterranean nests of an *Anthophora*, in keyholes,

and in the shells of landsnails, etc. Other bees (*Osmia rufohirta* Latr.) however have a narrowly specialised nesting-site (in the case of the bee mentioned, in snail-shells).

Those bees, on the contrary, which make their nest-cavity themselves have rather marked preference for particular habitats. A few of them, the 'carpenter-bees', burrow exclusively in objects of a vegetable origin. Some of them make tunnel in the soft heartwood of branches, usually dead ones (maple, hazel, ash, sloe-tree, etc.) others in plant-stems (mullein, bramble, raspberry, burdock, etc.). They obtain access to the soft heartwood only rarely by their own activity and, even when they can prepare entrance hole themselves (*Osmia tridentata* Duf. et Perris), they almost invariably use other burrows if they are available, while in other cases the burrow, at least in part of its course, follows a split or crevice. Other bees gnaw out their tunnels in the wood either when it is dead but still rather hard or when it is rotten (*Xylocopa, Lithurgus, Anthophora furcata* Pz.). Others again nest in galls and fruits (*Osmia gallarum* Spin., sometimes *Ceratina dupla* Say).

The great majority of solitary bees nest in the ground or in an earthy substratum; these are the digger-bees in a broad sense. As a rule they avoid places thickly grown with trees, shrubs or grass, but even with this restriction, the soil, local contours and the vegetation are so varied that one might expect to find here also a choice of nesting-site according to the species. As a matter of fact, some bees of this group (many *Anthophora, Colletes*) prefer to nest in steep slopes or, what amounts to the same thing, in the thickness of mudwalls or the courses of mortar in brick buildings. Certain bees (e. g. *Dasypoda plumipes* Pz., *Colletes cunicularius* L., some species of *Andrena)* nest only in loose sand or in very light soil. Many bees nest readily in quite open ground, e. g. on hard footpaths or garden walks (*Andrena florea* F., *Panurginus labiatus* Ev. and many species of *Halictus*), mainly to avoid grass-roots. The nests of many other bees are commonly found on the edges of woods and glades where the grass has not grown too close (*Systropha curvicornis* Scop., *Panurgus calcaratus* Scop.); nests of *Megalopta ipomaeae* Schrottky, were even found in moist ground in the semidarkness of a tropical forest. Finally in some species there is a tendency to build the nest with the entrance covered by a dry leaf, stone or piece of wood.

As a rule when the bee has found a suitable nesting-site it undertakes 'orientation-flights', i. e., it turns its head towards the nest and flies a zigzag course over it. If the bee is going to occupy a ready-made cavity it usually enters it and remains there one or two minutes before examining the neighbourhood. Two or three flights seem to be sufficient to establish the location of the nest firmly in the bee's memory. It has been shown by experiment (Malyshev, 1908) that the bees are here displaying a peculiar faculty partly based on the visual impressions of the individual.

The choice of nesting-site is not always final. Not infrequently, especially amongst the digger-bees, it happens that having begun their work in one place, they suddenly leave off without apparent cause and go to another which in its turn may be exchanged for a third; and this may be repeated several times. A similar phenomenon has also been observed in wasps.

## Preparation of the Nesting-site.

The work necessary for the preparation of the nesting-site consists either in accommodating the cavity itself or in transporting the suitable cavity (in this case a snail-shell) to a new place, where actual nesting will be begun. The latter behaviour is only known, however, from the careful observations of Ferton on one species of bee, *Osmia rufohirta* Latr.

The degree of complexity of the work of preparing the cavity itself varies greatly. In some cases, as for instance when the mason-bees build their nest on some large quite unenclosed surface, such work is not needed; but when a ready-made cavity is used (e. g. in the lodger-bees) it has to be more or less carefully cleaned. Inequalities of the walls are smoothed as much as possible and the debris so accumulated and any rubbish that may be in the cavity (remains of the pith of rushes, remains of the snail in a shell, debris of old cells, etc.) are carried out. The bees most studied in this respect are the *Megachilinae;* they fly away from the nest with the rubbish which they scatter about. Similarly the social bees are well-known to carry their rubbish some distance out of the nest. But some of the bees which

nest in ready-made cavities confine themselves to a very superficial cleaning of the site. Thus *Eriades campanularum* K. which lives in the straws of thatch, does not remove the old cocoons of the previous generation and *Anthidium florentinum* F. does not even bite away the endodermal partitions which sometimes entirely divide up the cavity of the rush occupied; the bee merely wedges its way between them. Not only numerous lodger-bees (*Prosopis, Osmia, Megachile*, etc.) but also many wasps (e. g. *Trypoxylon, Odynerus, Psenulus)* are attracted by the convenience of ready-made cavities; sometimes tenants, too, of other groups (e. g. *Dolichoderus, Forficula, Chelifer*, etc.). Sharp encounters between the competitors, often with a fatal issue for the invader, not infrequently arise from this eagerness to use ready-made cavities. This occurs, for instance, when the innermost whirl of a *Helix*-shell is occupied by one species (*Anthidium bellicosum* Lep.) and the mouth by another (*Osmia tricornis* Latr.) which nests at a different time of the year. When trying to get out the individuals of the first species are compelled to destroy the cells of the second and may themselves perish in doing so.

Much more work has to be done by those bees which make their own nest-cavity, for much more earth and dust has to be excavated than in the mere cleaning of an existing cavity. These bees do not fly far away from the nest with the earth but only carry it just outside and throw it away, or even simply leave it at the entrance. If the surface of the substratum in which the tunnel is made is too small (e. g. the end of a stem) or too steep (the face of a steep slope), the rubbish removed from the burrow does not accumulate near the entrance. On a more level surface, the particles carried outside remain at the entrance forming the usual hillock (tumulus), whose shape is always more or less and sometimes even quite characteristic.

This pile of earth may be quite loose and not pressed down at all by the bee (loose hillock). Consolidation proceeds with the course of time as a result of the influence of rain, wind and sun, and a solidified tumulus is formed. The shape of the tumulus much depends on the position of the nest-entrance, which may be either in the centre of the tumulus, or more or less eccentric or even right outside it. In this way one can distinguish central, eccentric and acentric tumuli. The configuration of the tumulus is further determined by the direc-

tion of the entrance tunnel which may be either vertical or more or less sloping, so that the tumulus becomes either asymmetrical, radial or bilateral (pl. III). In the first type no section of the tumulus is like any other (*Dasypoda plumipes* Pz.). When the symmetry is radial the tumulus has a centrally located entrance, a vertical entrance-canal and its general shape is crater-like (*Tetralonia malvae* Rossi). Here the tumulus is completely symmetrical about any plane passing through the entrance-tunnel, while a bilateral tumulus is symmetrical about only one such vertical plane, that which passes through the top of the pile, through the centre of the entrance and through the entrance-tunnel, which in this type of tumulus is almost invariably oblique (*Colletes cunicularius* L.). This sagittal plane divides the tumulus into similar right and lefthalves; a transverse vertical plane passing through the entrance hole at right angles to the plane of symmetry, further divides the tumulus into anterior and posterior halves. These differ in size and shape; the posterior one, for instance, may be higher (usually it is) or lower (e. g. *Systropha curvicornis* Scop.) than the anterior one. Again the latter may be longer than the former (shorter in *Halictus sexcinctus* F.). Further, on the anterior half there is sometimes a groove or path leading to the entrance [1].

According to the state of the entrance hole and also partly the character of the interior of the nest, one can distinguish closed, open and half-open tumuli. In a closed tumulus the aperture either remains constantly closed or is deliberately and regularly filled in by the bee (pl. III, fig. 6). From the condition of the entrance one can sometimes infer whether the bee is in or out of the nest (e. g. *Andrena ovina* Klug., fig. 58). In *Augochlora humeralis* Patton the entrance through which the bee originally burrowed into the ground (the primitive entrance) is only used for the ejection of excavated earth, while the bee itself leaves and returns to the nest by a specially made new entrance (the secondary entrance) which is also kept closed. If the earth which more or less closes the entrance is thrown off (usually on the anterior half of the tumulus only) at regular intervals, e. g. once in

[1] To determine the topography of a bilateral tumulus it must be approached so that the entrance tunnel slopes downwards towards the observer; then the right and left halves of the tumulus will be the same as those of the observer.

twentyfour hours, the tumulus is a half-closed one (*Systropha planidens* Gir.[1]). Finally there are nests in which the entrance is continually open as long as the work in the nest proceeds, except perhaps during the first stage of digging the burrow; such nests have open tumuli (*Colletes cunicularius* L.).

Although, as already mentioned, most tumuli are not built by the bee into a more solid structure, this is not the case with the part that forms the rim of the entrance hole. The particles of earth are here often so compressed and polished on the inner-side of the tunnel that a kind of tube is formed, quite hidden by the rest of the tumulus and usually clearly discernable only when the overlying earth is carefully cleared away (*Andrena ovina* Klug). The neatness and solidity of this tube show that it is the product of careful work and is not due merely to a natural adhesion of the earth. At present, however, it is not known whether the bee makes it simply by pushing apart and compressing the earth, while it is still damp, or by some special method such as moistening with water or saliva. When the nest is in dry ground the latter seems at least very probable (*Tetralonia malvae* Rossi).

The character of the tumulus, besides depending on the activity of the bee and the action of wind and rain, is also influenced by the topography of the nesting-site, by the nature of the vegetation growing there, by the quality of the soil (moisture content, friability, etc.) and by the activities of certain beetles (*Cicindela*, *Opatrum*, etc.). When these factors take effect in combination, especially if the bee had partially reconstructed the tumulus, the latter may lose its characteristic appearance. Other burrowing animals make tumuli over their burrows, but with a little experience, those of solitary bees are as a rule fairly easily recognized. Thus ants carry out earth in lumps so that their small tumuli (we are, of course, speaking only of these, not of ant-hills) are never very high. The small height of the tumulus is also characteristic of the burrows of many digger wasps (*Sphegi-*

[1] In some cases loose earth appears on the surface of the tumulus after considerable intervals when several cells have been made. This earth then covers all the old tumulus and forms a combined tumulus. Such tumuli are only found in combined nests (*Tetralonia malvae* Rossi, *Dasypoda plumipes* Panz.; Malyshev, 1930, p. 554; 1927, p. 133 and 139).

*dae*) which spread around the earth they bring up to the surface. Beetles (*Odontaeus armiger* Scop. and many other dung-beetles) on the contrary throw up very prominent tumuli built of well-defined earthen 'sausages', the characteristic result of their powerful efforts. The digger-bees, however, usually move backwards and eject only small quantities of earth at a time, behaving in this respect in a way intermediate between the digger-wasps and ants on the one hand and the beetles on the other. The digger-bee, *Osmia cristata* Fonsc., behaves just like a lodger-bee, for it takes the earth in its mandibles and flies far away with it to drop it. In all cases the tumulus of a digger-bee is the only external indication of the progress of work underground and therefore is of considerable interest.

In certain species the earth resulting from the excavation of the burrow or of other parts of the nest is used for building a special structure, the entrance tube and archway. The former is a direct prolongation of the burrow into the air and is attached to the substratum at its basal end, only its other extremity standing free. Its base may even stand on a special foundation (*Antophora parietina* F., according to Wesenberg-Lund). Entrance tubes may be made on horizontal, sloping or vertical surfaces, usually the latter. The outside of the tube is usually rough and the inside smooth.

The may be cylindrical or narrowed somewhat towards the free end and are often solid in the basal half, but latticed or with longitudinal slits in the apical part. In their origin they are probably a specialization of the tube which is sometimes built within the tumulus; if this is the case their object originally must have been to prevent the nest from filling up with earth. Such entrance-tubes have been observed in a variety of different solitary bees —*Anthophora* (*A. parietina* F., *A. crinipes* Sm., *A. abrupta* Say, *A. occidentalis* Cress., etc.), *Halictus maculatus* Smith, *Andrena morio* Brullé, *Eucera obesa* Dours, *Megalopta ipomaeae* Schrottky and *Euglossa nigrita* Lep. They have also been recorded in the social bees (*Trigona apicalis* Sm. and others) and in some wasps (*Odynerus* and *Ceramius*).

When the entrance-tube is fused with the ground along the whole of one side it forms the entrance-archway. This type of construction has been found in the bee, *Melitoma grisella* Cockerell and Porter,

and also in the African wasps *Ceramius capicola* Br., *C. caroensis* Br. and *Stizus clavicornis* Handl.

Thus we see that when bees prepare their own burrows each genus and species tends to make a nest in some way characteristic of it. The constructive powers of the bees are most fully and diversely developed when the substratum is of a type which gives least difficulty. The best medium is loose, not very hard soil, free from roots and stones and not traversed by cracks or fissures.

The subterranean burrows of solitary bees, considered apart from the structures at the mouth, are usually cylindrical tunnels with, at first sight, a very simple plan. The changes in direction and sometimes the nature of the walls of the burrow show, however, that it consists in most cases of different sections, which are put to different uses, so that it is in reality a compound structure (pl. IV). The burrow leading to the cells, at any rate to the first cell, is usually distinguishable into two parts — the main tunnel and the lateral one. The main canal is normally made at right angles to the surface of the nesting-site; thus on level ground it is vertical, while on slopes it may be inclined to a varying degree or even be horizontal. The main canal serves, therefore, to penetrate the substratum, to remove the cells from the danger of enemies, and to allow the larvae to develop in the most suitable conditions of temperature, humidity, etc.

The depth of the main canal varies greatly. Even within the limits of the same genus it varies between a few centimeters (*Andrena cineraria* L.) and forty inches (*A. bicolor* F., 101 cms.). In *Augochlora humeralis* Patton, the burrow may even attain the depth of four to five feet penetrating in some cases to the water-table. Further the same species of bee will dig its burrow twice as deep in loose soil as it will in hard ground; so, in *Colletes cunicularius* L., the entire length of the burrow in hard soil is 12 cms., while in loose sand it is 28 cms.

It may be noted here that the length of the burrow is partly correlated with the plan on which the cells are afterwards constructed. Thus the canal may reach its deepest point before the first cell is made and be gradually filled in as the work progresses (*Colletes cunicularius* L., pl. IV, fig. 7); conversely its depth may remain stationary or, in other species, increase as the cells are added. In a comparatively few

species only (part of *Halictus*, e. g. *H. sexcinctus* F. and *H. major* F. Nyl.) this correlation is less definite.

In some species the sides of the main canal are lined with soil-particles, taken either from the bottom of the burrow (*Andrena ovina* Klug, etc.) or from the surface (*Meliturga clavicornis* Latr.). This lining arises in a quite accidental way through the gradual transport of small particles from the bottom or the top of the burrow along its moisted walls. In a few cases, however (*Anthophora fulvitarsis* Brullé; *Megalopta*), the construction of a special lining of the main canal has been recorded.

The course of the main canal is often distinguishable into two sections, the entrance canal and the descending section. The entrance canal begins at the aperture and usually proceeds downwards though on vertical faces it may be constructed upwards, e. g. *Colletes daviesianus* Sm. It does not usually descend quite vertically, but even when it does (*Tetralonia malvae* Rossi, *Meliturga clavicornis* Latr.) it makes a more or less obvious angle with the succeeding section. This bend in the main tunnel prevents dust and rubbish from accumulating at the bottom of the burrow; the narrowing of the lumen near the aperture also contributes to this end. This narrowing near the entrance may be followed by a widening of the burrow forming the 'sentry-box' (*Ceratina callosa* F., *Xylocopa amethystina* F., *Halictus longulus* Sm.). Moreover the lower half of the entrance canal along its slanting part appears in *Anthophora bimaculata* Pz. and *Dasypoda plumipes* Pz., to be stopped up intentionally with loose earth or sand; sometimes it is entirely filled up (*Andrena ovina* Klug). *Augochlora humeralis* Patton besides the entrance canal which is always filled up, makes a secondary entrance which is direct continuation of the descending section, which in this species is vertical. Only rarely in typical subterranean burrows, no distinction is made between the entrance canal and the descending section (*Halictus major* F.).

The descending section of the main canal normally goes straight down into the substratum only occasionally making a few twists, probably to facilitate the ejection of earth and the movement of the bee alone the canal.

The lateral canal, so-called because even apparently continuous

burrows are best regarded as branched, generally starts from the lower end of the descending section. The lateral canal is never filled in while the work is in progress and being single the branching of the burrow is not obvious. It is usually horizontal or only slightly inclined, either upwards or downwards. It is obvious that the more acute the angle between the lateral canal and the descending section, the less chance there is of the former and the cell which lead out of it being blocked by earth falling down the burrow. *Tetralonia malvae* Rossi and *T. dentata* Klug are exceptional in making almost vertical lateral canals; as however, they make an arch-like section between the main canal and lateral, rubbish is excluded (pl. XIII, fig. 60). Probably the original purpose of the lateral canal was to prevent the cells from being choked with rubbish, and then to dispose them in substratum; but it also without doubt plays an accessory role in allowing the young bees to reach the open. Rarely (*Andrena ovina* Klug) the distinction between the lateral canal and the main burrow is so slight that it can only be made with difficulty by the use of special means. The length of the lateral canal is normally much less than that of the main burrow; sometimes (*Halictus sexcinctus* F.) this disparity is very great, the lateral canal being hardly larger than a cell or even smaller. The width of the lateral canal starts the same as that of the descending section but further along it usually becomes much narrower.

As a rule the end of the lateral canal is specialized for distance about equal to the length of cell to form an anti-chamber which is narrower than the rest of the canal and usually has special walls (absent in *Dasypoda plumipes* Pz.). The walls of the anti-chamber normally have the same nature as the external walls of the cell, but in *Colletes* they have an internal lining. There is reason to believe, however, that the special walls of the lateral canal are made at the same time as those of the cell (*Anthophora acervorum* L.).

In some species the lateral canal instead of narrowing at its end becomes broader and may merge indistinguishably with the cell (*Halictus major* F.) without the usual sharp border. The enlargement of the end of the lateral canal, if it is distinct from the cell, represents the first stage of an breeding-chamber, into which, as the work progresses, all the cells will open. In still further specialised forms (*Halictus calceatus* Scop., *Augochlora humeralis* Patton) the breeding-

chamber is enlarged so as to surround the cells themselves (fig. 65). This sort of lateral canal may be called common is distinction from the particular one where the lateral canal leads to one cell only.

It has already been stated that the lateral canal usually begins at the lower end of the descending section of the main burrow. There are a few exceptions to this — species in which the main burrow is continued downwards beyond the point where the lateral canal branches off. This prolongation may be quite short such as the so-called 'heel' in the plaster casts that have been made of the nests of *Colletes*. In other species, however, this part of the burrow is rather elongate and forms a special supplementary canal, which may even be longer than the descending section of the main burrow (pl. IV, fig. 10), and it may be the starting point of new lateral canals, either particular or common. Other species (*Halictus calceatus* Scop., *H. quadricinctus* F.) which make a long supplementary canal have a single lateral canal which is a common one. There is some evidence (Smith, 1901) that the bee takes building material from a certain area in the supplementary canal so that small pocket is formed here (*Augochlora*). The supplementary canal is usually a vertical prolongation of the descending section but it may be somewhat inclined.

In the not uncommon case where the length of the main burrow increases with the number of cells, there arises between the first and later constructed lateral canals a special section of the burrow, viz. the intermediate canal (pl. IV, fig. 8, *c-d*). The gradual enlargement of this canal at regular intervals is its most characteristic feature. It is usually more oblique than the descending portion of the main burrow and in *Tetralonia malvae* Rossi where the descending section is itself very oblique, the intermediate canal is nearly horizontal. The intermediate canal is usually bent into a number of zig-zags, each bend being directed towards the end of the lateral canal given off at that point. If the number of cells is large the intermediate canal may be longer than the descending section of the main canal.

Some digger bees, instead of making the typical burrows with complex canals as described above, excavate nests so simple in structure that even a lateral canal is absent, though the soil conditions may be favourable for digging. Thus *Osmia papaveris* Latr. — a bee of the subfamily *Megachilinae* whose members, though very skillful in some

ways, are not clever at digging —, merely excavates a cylindrical burrow in the ground; the burrow is as straight as a well and is enlarged at the bottom for the cell. The choking of the entrance is guarded against by lining the burrow up to and sometimes over the rim with small pieces of poppy petals. Other species of *Osmia,* belonging to the *O. papaveris*-group, make similar nests.

If one attributes the simplicity of these *Osmia* nests to the lack of special skill in excavation, then the lack of complexity in the nests made in hard soil or in mud walls is probably rather due to the hard unyielding nature of the substratum. Here the mandibles and the brushes of hair on the legs of bees are scarcely sufficient tools, and it has been observed that many bees which nest in this type of soil bring a supply of water in their crop to soften the earth as their work proceeds. Many journeys have to be made to replenish their supply of water, so it is not surprising that the burrows are shallow and have little complexity. Such nests are made by some species of *Colletes,* many of *Anthophora,* also *Emphor,* etc.

In the case of carpenter-bees the influence of the substratum is even more marked. The canals may be either short or long but in the latter case always run along with the grain of the wood or along the pith of plant stems. Thus nests in a vegetable substratum consist mainly of straight or of but slightly bent canals (pl. IV, fig. 11). Further the bee has little power to decide whether the direction of its burrow shall be horizontal or vertical, this depending on the position of the plant stem in which the burrow is made; in the case of a burrow started in the centre of an erect stem of *Verbascum,* for instance, it can only decide whether to tunnel upwards or downwards, usually (*Ceratina callosa* F., *Osmia tridentata* Duf. et Perr.) the latter is chosen.

The diameter of the tunnel appears to be independent of the nature of the substratum and to depend rather on the size of the bee and on type of nest which is being excavated. Canals made in plant stems are sometimes so narrow that the bee cannot turn round inside the nest and has to back out if it wishes to do so. When nests are built in soft or in very rotten wood, it may be possible to distinguish an entrance gallery, narrowing to the entrance itself, a main canal, and one or several lateral canals, each with its anti-chamber (*Anthophora*

*furcata* Pz.) or without it. In these nests there is sometimes and an intermediate canal (*Xylocopa valga* Gerst.).

Nests built in narrow plant stems have at the most, besides the single tunnel for all the cells, only a constriction of the canal at the entrance and a sentry-box (*Ceratina callosa* F., *Xylocopa amethystina* F.) [1].

For obvious reasons the lodger-bees are unable to make canals of definite width, length or shape; at the most they can only clean out the cavity they have adopted. Their ability lies in another direction; by making a transverse partition, they delimit the nest canal proper from the further prolongation of the adopted cavity, a part of which may not be needed for the nest itself. A similar transverse partition is made by some species near the entrance, where it serves as a door while the cells are being made. A membranous door of this nature is made by *Prosopis punctulatissima* Sm. and by *P. variegata* F., the latter species using the empty burrows of earthworms or of *Halictus*.

When a solitary bee has finished making its nesting site in one of the ways we have been describing, the work of making the cells begins.

## The Cells and their Construction.

The larvae of all bees, solitary, social and parasitic require a separate cell for their development. The cell is the most important and indeed the only essential part of the nest; in some mason-bees the nest consists merely of several cells built side by side. The cell of a bee is essentially only a completely enclosed space in which all the necessary for the development of the young bee has been provided. Its main and, normally, only purpose is to isolate the growing individuals from one another and to protect them from harmful external influences. A typical cell is therefore inhabited. According as a cell contains a male, female or worker bee, it may be spoken of as male, female or worker cell.

Comparatively rarely a few of the cells of a nest are not used to house larvae, but have some secondary function indirectly connected

[1] No ante-chambers have been described for cells in nests in plant stems; nevertheless it is most probable that they occur (cf. *Prosopis dilatata* K.).

with the welfare of the young. These uninhabited cells may be used to protect the larvae against parasites (*Osmia emarginata* Lep., *Anthophora acervorum* L.), or they may be used as receptacles for additional food (as in the social bees) or, finally, as a device to allow the young bees to emerge from the nest (*Ceratina callosa* F.). Thus these uninhabited cells may be divided into protective, storage and supplementary cells.

Besides bees, most wasps characteristically bring up their young in cells. There are a few exceptions, but they are rare and this behaviour appears to be either optional or else a survival from a very primitive condition. As examples one may mention those wasp-larvae which have not infrequently been found on freely moving spiders or larvae (Adlerz, 1910, 1911). The construction of cells is also observed amongst Lamellicorn beetles (*Scarabaeidae*). Here the parallelism with the habits of bees may be very striking (cf. *Lethrus apterus* Laxm., pl. X, fig. 51). The ants and the termites in which also the care of the young is highly developed, behave differently, for they do not keep their larvae in cells, but «nurse» them and carry them from place to place.

*The plan of a bee's cell* is very simple (pl. V, fig. 12). It is shaped, as a rule, like a pot with one end at first open but later, as far as is known, this too is always closed. The parts of a cell whether of a bee or a wasp, are: the walls and the cavity. The anterior wall is where the bee enters the cell to provision it and to lay the egg: the barrier (cell-cover) afterwards built here finishes the enclosure of the cell. Opposite this is the posterior wall, which is joined to the anterior one by the longitudinal walls; these are normally distinguishable into an upper, a lower and two lateral walls. In some cases the posterior and the lateral walls are sharply marked off, but in others they pass insensibly into one another.

A line equidistant from all the longitudinal sides and joining the centres of the two end walls is the longitudinal axis; it is usually straight, but in some species it is curved like an arc or parabola (fig. 12). The horizontal axis of the cell is a horizontal line drawn through the longitudinal axis at the widest point of the cell. Where these axes intersect is the centre of the cell, which normally falls either at the middle of the longitudinal axis or between that point and the

beginning of the posterior third. Another line drawn through the centre of the cell at right angles to the horizontal axis is the vertical axis. As will be explained further on, the position of the axes depends on the general orientation of the cell. The horizontal, vertical and longitudinal axes respectively, measure the greatest width, height and length of the cell.

Although all cells are built on the same simple main plan, yet a wide range is found in the dimensions of the axes, in the material of which the cells and their inner lining are made, in the origin of the cavity in which they are built, etc. In the following paragraphs these differences, which are to some extent characteristic of genera and even of species, will be considered in detail.

*The Shape of the Cells.* The shape of the cells may be described in several ways. First the proportions of the axes to one another have some importance. In this way two types of cells may be distinguished: the elongate, in which the longitudinal axis is longer than either the horizontal or the vertical axis which are of the same length, and the shortened, in which one or both of the latter axes is as long as or longer than the longitudinal one. The great majority of the cells are elongate, usually more or less egg-shaped or elongate-cylindrical. The commonness of this type is easy to understand, for it corresponds to the shape of the body of a bee (or a wasp). Shortened cells are comparatively rare, e. g. the globular cells of some of the Meliponid bees, and the short cylindrical ones of *Osmia rufa* L. when nesting in very wide-stemmed rushes, a few other species make domed cells which are also transverse. The young bee is only able to develop in the shortened cells because it lies obliquely across the cell, instead of along the longitudinal axis, or because, as in some wasps *(Eumenes)*, the body is sharply bent near its middle. Finally a few of the shortened cells are not actually used for the young but for other purposes.

Some bees, especially digger bees, keep their cells very constantly to one shape (cf. the cells of *Andrena bimaculata*, pl. XII, fig. 59) in other bees accidental peculiarities of the nesting site alter the shape of the cell considerably (*Osmia coerulescens* L., pl. XV, fig. 67, etc.). Thus one may distinguish between homomorphous cells, whose shape never varies, and heteromorphous ones whose shape varied with the external conditions.

The majority of cells (pl. V, fig. 15-17), are arranged with bilateral symmetry. The plane of symmetry is the sagittal one passing through the longitudinal axis which is bent in the form of a parabola. Of this type are the cells of *Colletes cunicularius* L., *C. compactus* Cress., *Andrena ovina* Klug and *Anthophora acervorum* L. with many others. Not rarely the cells are radially symmetrical, so that all planes passing through the longitudinal axis divide the cell into equal halves; elongate cylindrical or oval cells of this type are seen in such bees as *Tetralonia malvae* Rossi, *Systropha planidens* Gir., *Anthidium florentinum* F., etc. Quite a number of bees, further, make assymmetrical cells which are also nearly always heteromorphous (*Osmia cornuta* Latr. and *Prosopis* species).

A more fundamental division of cells may be based on their relation to the surrounding substratum and in this way two main groups of cells can be differentiated. In the first the shape of the cell depends entirely on the cavity in which it is made, so that the cells cannot be constructed freely outside. Here only the shape of the anterior end is determined by a wall built by the bee itself. In building the latter the bee is unable to exercise much skill, it merely determines the longitudinal extension of the cell, i. e. if the wall was not built the longitudinal axis could be produced forwards indefinitely. The posterior end of the cell, in the vast majority of species, depends on the nature of the cell cavity; often this end of the cell is the anterior end of the cell built just previously.

It is only when the nest cavity is unusually deep and under certain special circumstances (double partitions) that a special wall, without which the posterior end of the longitudinal axis would extend indefinitely, is constructed. The longitudinal walls of the cell naturally show the greatest dependance on the form of the cavity. In typical cases this dependance is complete: the sides of such cells are limited by the surface of the cavity, whose width determines the length of the two transverse axes of the cell. Much more rarely the size of the cell is limited to a certain extent (see further on) by a special partition, whose shape is independant of the cavity. Since in all these cases the shape of the cell is dependant mainly on that of the cavity, they may be called dependant or allomorphous cells.

In the other main group of cells the shape does not entirely or

even mainly depend in the cavitv occupied (fig. 57). The independance is so great that the cells need not be constructed in a cavity at all, but on a level or even on a convex surface (*Chalicodoma rufescens* Pérez, *Osmia globicola* Stadlm., *Anthidium strigatum* Pz., etc.). The independance of the shape of the cell is sometimes complete, when all the walls of the cell are built by the bee itself. A certain limitation of this independance is not uncommon, though unlike allomorphous cells, the shape of the cells in the second group is determined on one side only, viz., the side resting on the substratum. In other words, only one of the four ends of the transverse axes is limited by the surface of the substratum, the other three by special walls whose shape is independant. It is therefore, appropriate to call the cells of the second group independant («free») or automorphous.

As in all our classifications of living nature, this division of cells into dependant and independant ones is not absolute, for intermediate types are known. These «half-free» cells are found when two sides of the cells are determined by the substratum, while special walls whose form is quite independant of the form of the cavity, limit the remainder. To put it differently, in the intermediate cells two of the four ends of the transverse axes are limited by the surface of the substratum and two of them by special walls. It must, however be noted that these cells of an intermediate type occur sporadically and that the author knows of no species which constructs these «hemimorphous» cells exclusively. There is, therefore, no reason to make a third group equivalent to the two former; especially since it is easy to draw quite definite conventional limit between the dependent and independent cells. Thus when no more than four ends of the axes (usually only one) lie on specially built walls, the cell may be called «dependent», in a «free» cell five or six axis ends will lie on walls constructed by the bee.

The freedom of the cell from the substratum may be expressed in a formula, giving each of the ends of the three axes a symbol, a «free» end is given a positive sign and a «dependent» end, limited by the surface of the substratum, a negative one. These symbols are as follows:

*a*.—The anterior end of the longitudinal axis.

*b*.—The posterior end of the longitudinal axis.

*c*.—The right hand end of the horizontal axis [1].
*d*.—The left hand end of the horizontal axis.
*e*.—The upper end of the vertical axis.
*f*.—The lower end of the vertical axis.

The following are some of the most characteristic formulae:

1. $(+a-b-c-d-e-f)$.
2. $(+a+b-c-d-e-f)$.
3. $(+a-b-c+d-e+f)$.
4. $(+a+b-c+d-e+f)$.
5. $(+a+b+c+d+e-f)$.
6. $(+a+b+c+d+e+f)$.

The left hand column consists of dependent cells (1-4 positive indices), the right hand one of «free» cells (5 6 positive indices). The first formula, in which there is the greatest dependence on the substratum is specially characteristic of the cells of digger-bees, carpenter bees and lodger bees; the second formula represents some cells of lodger bees (e. g. the first cell of *Osmia rufa* L. when the nest cavity extends into a gallery behind the cells; pl. V, fig. 19) and of carpenter bees (often *Ceratina callosa* F.). The third formula represents cells built in a three-sided cavity; such lodger bees, which nest in wide cavities, sometimes use. The fourth formula expresses a cell built in a two-sided angle, shaped like a quarter of a cylinder (rarely in *Osmia coerulescens* L.). The two remaining formulae represent mason-bees cells, the fifth a cell of which one entire side is resting upon a slightly concave or level surface, and the sixth a cell fastened to a level or convex surface by a part of one side only.

It is quite possible of course that mason-bee normally building its cells according to the fifth formula may occasionally build one or two cells after the fourth or even third formula, lodger bees also sometimes vary their behaviour in this way. Nevertheless the difference even between cells similar in shape will be important, thougth in another way: in the first case the shape of the surface of the substratum (e. g. if indented in a two or three sided angle) prevents the mason-bee from showing in any great measure its skill in building; in the

[1] If the cell is examined with the anterior end facing the observer then the right end of the horizontal axis will correspond to his right and the left hand end to his left.

second case, on the contrary, the unevenness of the substratum favours the skill of the lodger bee. In other words in the mason-bee there is a tendency to simplification, and in the lodger bee to complication of the work. According to the convention, however, a cell built after the fourth formula will still be called a dependent one.

*The Walls of the Cell.* We have already said that the cell-cavity is sooner or later surrounded by walls on all sides. Such cells may be therefore called closed or «holotichal»[1]. Only exceptionally when empty, uninhabited cells are being rebuilt, does the enclosure of the cell-cavity form a single continuous activity, uninterrupted by other work. Usually at least on the anterior side, the cavity of the cell is only closed by a special wall or cover after the cell has been stored. Consequently the closing of the stored cell as well as the construction of the cover itself will be treated further on. The cell, therefore, until its provision has been completed remains open at one end. There are, however, a few exceptions known to this rule, i. e. species in which while the cell is being stored or even when still empty it is temporarily closed; thus *Anthidium florentinum* F. as the author has observed bends the brim of the anti-chamber inwards and so closes the cell every time it leaves the nest; on returning the bee carefully opens it and then usually goes in backwards. This habit of temporarily closing the cell is also the rule amongst the humble-bees (*Bombus*).

Typical open or hemitichal cells are built by the social wasps (*Vespidae*) and by at least some of the solitary ones closely related to them (*Odynerus laevipes* Shuck., Malyshev, 1911, p. 13). Under these circumstances the front wall is built by the adult larva so that the cover here is a part of the cocoon and not of the cell-wall. Brauns (1902) records of a bee from the Cape Colony, *Allodape* sp., related to *Ceratina*, that the young larvae develop in the common canal of the nest in a plant-stem which is not divided into separate cells by partitions. The paper is, unfortunately very brief and contains no indication of the order in which the parts of the nest are constructed. It is possible, however, that the same thing happens that I have des-

[1] Zoologists have already made some use of this term; the supposed covers of the nidamental glands of the ammonites are called aptichae. Greek teixos, a wall.

cribed in *Ceratina callosa* F. where the individuals that have developed earliest at the bottom of the nest, make their way to the outside, destroying the partitions separating the cells which lie above. As a result the occupants remaining continue their development in sections of the canal divided only by the debris of the partitions, so that by degrees they sink downwards in the nest. If these debris were scanty and the history of the nest were imperfectly known, it might be thought that there were no partitions at all. If a real lack of partition should be confirmed in *Allodape,* we should then have an example of open cells in the bees also [1].

Very often the circular and somewhat narrowed opening of the cell is surrounded by an evident rim or mouth. This cannot be the case when the lateral canal is not terminated by an anti-chamber of the cell, but by a terminal broadening (see above). However on the lower side of the entrance to the cell of *Colletes* (*C. cunicularis* L., etc.) there is a wellmarked threshold of membrane while in *Prosopis,* as far as I know, it is rudimentary (pl. V, fig. 12, *p*).

The back end or bottom of the cell together with the longitudinal walls, i. e. the ceiling, floor and sides are usually the result of one building operation, not interrupted by any other work. A peculiar divergence from this rule is found in *Chalicodoma* (*Ch. muraria* F., *Ch. pyrenaica* Lep.) which alternately build the longitudinal walls of the cell and accumulate provisions in it.

In their origin the walls of bees' cells, generally speaking, differ greatly from each other. In this respect a distinction must be made between simple or allotichal walls and special or autotichal walls. The former are simple the sides of the cavity occupied by the cell, neither solidified nor impregnated by the builder, perhaps only smoother; the latter are walls which are specially built by the bees, so that the admixture of some kind of cement and removal of particles of the building material usually may be detected. In bees the cells are most rarely so simple as to be delimited entirely by allotichal walls. Such allotichal cells are found only in *Lithurgus* (*L. fuscipennis* Lep., Malyshev, 1930) and certain wasps in which the care of young is scarcely developed (*Scoliidae*). In the bees, on the contrary,

[1] For the construction of the cells of *Lithurgus fuscipennis* Lep. see also below.

cells with special walls erected by the builders themselves, i. e. autotichal cells, are very common and quite characteristic.

However not infrequently, chiefly when ready-made cavities are being used, the walls of one cell have double origin — some of them, for instance the bottom and the cover (the latter always), are autotichal and the rest allotichal. These therefore, are heterotichal cells. These are seem most characteristically (in an opened up nest) when the autotichal walls, consisting of simple partitions separating one cell from another, divide the nest-gallery transversely into a series of compartments. In this case the transverse partitions are usually straight and more or less perpendicular to the longitudinal axis of the canal. One instance is known however of oblique transverse partitions (according to Nielsen in *Osmia solskyi* Mor.). Here the nest cavity is inclined (the nest is in the rushes forming a thatched roof) and the partitions are vertical. From the morphological point of view, the simple transverse partitions may be formed by either the bottom or by the roof (or by both) of the neighbouring cells (usually in *Osmia rufa* L., fig. 68, etc.).

Sometimes two simple partitions are separated by a empty compartment which is either about as big as the cavity of the cell or else considerably bigger or smaller (usually in *Ceratina callosa* F., pl. XV, fig. 69, often in *Osmia parvula* Duf. et Perr., more seldom in *Eriades florisomnis* L. and other bees; among wasps usually in *Odynerus murarius* L., *O. bifidus* Mor.). Occasionally, apparently as an aberration, the number of empty compartments separated from each other and the neighbouring cells by solid partitions may be as many as two or three or even more. These are adjoining partitions of double, triple or greater complexity. The double partitions, at least in some cases (*Odynerus murarius* L. and sometimes *Ceratina callosa* F.) correspond morphologically to true cells (protective or reserve cells).

Those cells in which the same wall is made up of parts of different origin, must also be called heterotichal. This is almost peculiar to the longitudinal walls of the cell; in these cases both the autotichal and the allotichal parts of the cell-wall have usually a very different structure and generally are very variable, e. g. in the shape of bands, grooves, network, etc. (*Osmia adunca* Latr., sometimes *O. rufa* L., etc.).

Fabre has discovered in a number of species of *Osmia* (*O. tricor-*

*nis* Latr., *O. cornuta* Latr., *O. latreillei* Spin., *O. tridentata* Duf.) the peculiar habit of constructing a rounded «threshold», or a transverse partition, leaving a loophole for themselves, at the entrance of the cell when this is situated in a broad burrow or ready-made cavity (pl. V, fig. 13). Many of the authors who have written about the nesting of *Osmia* do not mention this habit, but I have observed it often in *O. rufa* L., *O. solski* Mor., *O. tridentata* Duf. et Perr., and I am of the opinion that it is peculiar to all the *Osmia* species that build heterotichal cells. The order of work in the construction of this «threshold of Fabre», is as follows: first the bottom of the cell, then the threshold, afterwards the provision of the cell and lastly its closing. This proves conclusively that the threshold must be of the same nature, as the longitudinal walls, which in the species under discussion are allotichal in the greater part of its extent; only the part of these walls nearest the cell entrance is autotichal. Thus «Fabre's threshold» represents the vestiges of the once continuous autotichal longitudinal walls. The species of *Osmia* which now build heterotichal cells apparently formerly developed in autotichal cells. It is not without interest to note that in the wasps, at least those of the group *Diploptera*, the order was apparently the reverse: the heterotichal cells gave rise to the autotichal ones (Malyshev, 1911).

From the preceding discussion it follows that the autotichal walls, which delimit the cell-cavity without the participation of the substratum, may be termed free walls, while allotichal and autotichal walls, in so far as they are merely a coating or lining are dependent walls.

*The building material.* Since bees in building their nests use all kinds of cavities, it is quite clear that the nature of the allotichal walls varies in the same way, and need not be considered here. The material of which the autotichal walls is made is also very variable. The first important distinction lies in whether the bee procures the material in the nest itself, or close at hand, or whether it is brought in from outside. There are thus two working methods and two types of cells: the endostoechal and the ectostoechal [1]. It appears that there are no definite exceptions to this rule. If a mixture of the two

[1] στοῖχος, material.—This classification, of course, is not in any way disturbed by the existence of heterotichal cells which may be endostoechal *(Ceratina callosa* F.) as well as ectostoechal *(Osmia rufa* L.)

materials sometimes occurs it is either quite casual or else it is only different cells or quite different parts of the nest which are made of mixed material. Thus for instance, when special walls made of sticky material («green mastic») are fastened to the friable walls of a cavity (in earth or in the pith of plants) fragments of the walls may become detached and be mixed up with the mastic (*Osmia maritima* Friese, *O. tridentata* Duf. et Perr.); on the other hand *Trigona* builds the cells, in which the young are reared, of material produced in the nest (i. e. wax), while other cells (i. e. those in which honey is stored) are made of resin brought from outside. Lastly in *Osmia parvula* Duf. et Perr., the autotichal walls of the cells (the transverse partitions of the nest canal) consist of ectostoechal material («green mastic») and the accumulation usually found between them of endostoechal material (viz., shavings of the pith of the stem used for the nest — apparently only because the nest is insufficiently cleaned out). To the same cause must be referred the apparent mixture of material in the nests of the wasp *Odynerus laevipes* Shuck., in which the open earthen cells are sometimes divided by accumulations of pith-shavings, at least in so far as these accumulations do not result from the activity of the larvae (cf., p. 228). It cannot, further, be considered as a refutation of the general rule that *Apis mellifera* L. closes the cells filled with honey with covers made of a mixture of wax and propolis; both materials are taken by the bee from stores within the nest, i. e. that already at hand, matters moreover are complicated since the individuals of the hive divide the labour both of providing material and of its employment. Such mixtures of materials as are found in the nests of humble bees also appears to be either accidental or the substances mixed are used in different parts of nest [1]. But we need not expect to find a complete division in this respect, since the bees which learned to

[1] It is not uninteresting to note that *Apis mellifera* L. which builds endostoechal cells brings the ectostoechal material (propolis) which it uses chiefly for closing chinks, coating the roughness of the walls, etc., on the tibiae of the hindlegs i. e. in the same way as hard food (flower-dust) is transported to the nest. The solitary bees, as far as I know, carry materials for building their entostoechal cells with their forelegs or mandibles or hugging them to the body with all their legs. It would be interesting to know in what way the resin is carried to the nest by *Euglossa* whose hind legs are provided with «baskets» as those of the social bees.

procure their building materials outside the nest, no doubt previously got them from within. We shall return to this question and in this place it is only necessary to emphasize the psychological difficulty preventing the bees from employing both methods simultaneously.

There are, however, substances used in moistening dry materials which are sometimes used in building either endostoechal or ectostoechal cells; these are water and saliva, insofar as the latter is used for cement. The way these liquid materials are used has partly been explained already and will be dealt with again later.

Let us now consider the endostoechal cells. The sources of building material in this case may be either the walls (mineral or vegetable) of the nest-cavity or the glands of the builder itself. Most often (in the very large majority of digger-bees and in some carpenter-bees) material obtained from both sources is used in building any one cell. The mixture is not so complete but that two layers, the outer and the inner one closely joined together may be distinguished. In the former the substance of the substratum always predominates and secretions of glands (or simply water with and admixture of saliva) acts only as cement, permeating the more or less compacted walls to a variable but usually slight extent (about 1·2 mm.) The second layer, forming the real inner lining of the cell consists (apart from accidental mixture of material) entirely of secretions of the bee's own glands. Owing to this circumstance the interior of the cell appeares glossy or polished. Further investigation of the inner lining of endostoechal cell shows that it may be of two kinds. In one type (*Andrena, Halictus, Tetralonia, Panurginus*) it is silklike, indissoluble in either chloroform or sulphuric ether and not melting when heated, in the other (*Anthophora, Melitta, Macropis*) it is waxlike, soluble in ether and chloroform and melting when slightly warmed. These linings differ greatly in their origin. As far as is known (though this is only in a few species) the silky substance appears to be secreted by the bee from its mouth and the waxy one from its abdomen. The former at least is known for *Prosopis pilosula* Pz. (Ferton, 1897), for *P. punctatissima* Sm., according to my observations and *Chilicola inermis* Fries (Claude Joseph, 1926), while the latter I was able to follow in detail in *Anthophora acervorum* L. (1928).

Very much less frequently the walls of endostoechal cells are built

with material of one kind only, either with material taken from the walls of the cavity (*Systropha*, *Rhopites*) or with material secreted by the bee itself (*Colletes, Prosopis, Chilicola, Lonchopria*). The solitary bees using such uniform material only build dependent cells and therefore the walls so made are like a lining or at most like a transverse partition or cover. The social bees, on the contrary appear to be quite alone in constructing independent cells built exclusively or chiefly from secretions of their own glands (wax glands). Sometimes indeed, cells built partly of wax have been described in solitary bees (*Anthidium limbiferum* Mor., *Euglossa*), but these bees belong to those very genera which are characterized by the instinct to collect building materials outside the nest. Therefore at present it is better to assume that they collect the «wax» somewhere else and do not secrete il themselves. An endostoechal cell of a peculiar type for a bee is constructed by *Dasypoda plumipes* Panz., its cell has no lining, the cover only in this case is autotichal (pl. VI, fig. 23); such a cell on the other hand is very characteristic of the solitary digger-wasps.

Ectostoechal cells are found chiefly amongst lodger and mason bees. The material of which ectostoechal cells (or, more precisely, of their special walls) are built may be of a mineral, vegetable or animal origin. Of the first type are ready-made plaster made out of mud (*Osmia rufa* L., *O. tricornis* Latr.) and the cement prepared by the bee itself from dry earth and saliva (*Chalicodoma*). Sometimes besides dust larger particles are also used, e. g. grains of quartz, etc.

Of vegetable origin are such natural secretions of plants as resin *Anthidium septum-dentatum* Latr., *Eriades truncorum* L.), gum (*Osmia exenterata* Pérez) or various sticky juices (*Osmia glutinosa* Giraud, *Eriades florisomnis* L.). Of this nature most probably (see above) also is the wax-like matter found in the cells of *Anthidium limbiferum* Mor. Much more frequent use however is made of fragments of plants, which are sometimes minced up. Of the latter, the most common type is the green mastic, consisting of chewed or shawed off bits of green plants. Such are the oval, round or irregularly shaped pieces of leaves used by many *Megachile* species, the ribbon-like pieces of leaves cut out by *Trachusa serratulae* Panz., or the entire leaves cut by *Megachile* from young shoots of *Vaccinum myrtillus*. Besides the green tissues other vegetative parts of plants may also be used in

building of the nest. Such are, for instance, the hairs scratched by some bees off still living (*Anthidum manicatum* L.), or dead and dry leaves and stems (*Anthidium diadema* Latr.); such also are the pieces of the epidermis, dyed with betulin, cut by our *Megachile analis* Nyl. from the bark of birch. Certain species of *Osmia* (of the group of *O. papaveris* Latr.) and as an exception *Megachile* (*M. imbecilla* Gerst.) use parts of the petals and corolla of various coloured (red, yellow, white) flowers. Il appears that even the petals of compositae are sometimes gathered. The pollen also may be used to line cells [1] as Strand (1909) records in *Ptilothrix plumata* Sm. Lastly *Anthidium florentinum* F. avails itself in some cases of the pappi *Compositae*, sometimes with seeds attached.

Building material of an animal origin is only seldom brought in from outside when the cells are being constructed. The following may be used: first the excrement of mammals - oxen, camels (*Osmia turensis* F.), hares or sheep (*O. spinulosa* K.) and perhaps fox, as well as the saw dust of the larvae of *Buprestidae* and longicorn beetles (*Megachile bombycina* Rad., partly). Further firm fragments of animals are not infrequently found; heads of ants (in *Anthidium quadrilobum* Lep. and *A. latreillei* Lep.) or the small shells of snails (*Osmia caementaria* Gerst. sometimes). In the nests of *Anthidium florentinum* I have found the down of birds, but this is an exception. It may be added that wasps of the genus *Agenia* sometimes use cobwebs as building material.

The three types of building material mentioned may be used either separately or together in various combinations. The following are some examples. The outer layer of the walls of the cells of *Megachile ericetorum* Lep. is built of mortar of mineral origin and the inner lining of resin; in *Trachusa serratulae* Panz. (fig. 66) the former is made of ribbon-like pieces of leaves and the latter of resin; the only known cell of *Osmia ononidis* Ferton was built on the outside of pieces

[1] If this is really so, i. e. the lining of an endostoechal earthen cell with pollen is a special act of the bee and if the pollen is brought for this purpose and made use of even before the cell is provided with food (the same pollen but made into cakes) — then we must admit that we have before us a heterostoechal cell. But the existence of such cells among the bees cannot as yet be considered as proved.

of petals (first of yellow ones and towards the inside of red ones) of different plants; on the inside it was lined with mortar; the nests of *Anthidium quadrilobum* Lep. consist of resin, on the outer side of which are set in small lumps of earth and the dry heads of ants (Fabre) [1].

*The Cavity of the Cells.* When a bee or wasp nests in a ready made cavity or on an open surface, then building a cell it merely isolates in one or the other way the area of free space available; but when it prepares the nest cavity for itself, it has to create the actual cell-cavity (or cavities) which are required. The cells of the first kind are therefore allocoelous, and those of the second kind autocoelous. The former are found in the lodger-bees, the majority of mason bees and rather exceptionally (sometimes when parental nests are utilised) in other bees; the latter, as a rule, are found amongst the digger-bees and carpenter bees and rarely in the mason-bees (*Anthidium laterale* Latr., *Halictus 4-cinctus* F., *Anthophora balneorum* Lep.).

The volume of the cell-cavity is correlated to some extent with the size of the builder, but is also partly determined in other ways. In a general way, however, one can distinguish, besides the usual moderately capacious cells, narrow and wide ones. Thus in *Tetralonia malvae* Rossi, the cell is so small that the adult, full fed larvae fills it completely; if such a larvae is taken out of the cell it is impossible to put it back (pl. V, fig. 16, and pl. VI, fig. 23). The larvae of *Dasypoda plumipes* Panz., at the same stage of development lies on the contrary quite loosely in its cell. The special causes influencing the dimensions of the cell-cavity are first the mode of provisioning and the quality and quantity of the food. The operation of provisioning cells being the theme of the next chapter, we will only remark here that cells of wasps are generally larger than those of bees, which are provided with less bulky food. In the same way the modes of provisioning cells are widely different in *Tetralonia malvae* Rossi and *Dasypoda plumipes* Panz. (see further on). Sexual demorphism in size is also of great importance.

[1] Ferton believes the latter to be accidental inclusions. The fact, however that both Ferton and Fabre found this inclusion in the same place the outer layer of the cells (or their general coating) favours the idea that this is a regular habit.

Thus the male cells are usually conspicuously smaller than the female ones, corresponding to the normal difference in size in the sexes. Where the relation is inverse (*Anthidium* and other genera) the male cells exceed in size those of the female. Moreover it ist well known that the worker cells of *Apis mellifera* L., are smaller than those of the male (drone) and especially than the large female (queen) ones. When the difference in size between the sexes is inconsiderable, the cells scarcely differ in this respect (*Osmia tridentata* Duf.). Sometimes there is a tendency to have cells of constant volume by thickening the walls to fill up the greater part of the cavity occupied when this is larger than usual [1].

*Orientation of the Cells.* The position of a cell in space is expressed by the relation of its longitudinal axis to the horizon. The longitudinal axis of the cell may be horizontal («horizontal» cell), the axis may be at an acute angle to the horizontal («inclined» cell) sloping downwards or upwards according as to whether the posterior end of the axis is lover or higher than the anterior. Lastly, if the longitudinal axis of the cell is vertical the cell is an «erect» one, when the bottom lies below the cover, or «inverted» when the bottom lies on top.

Generally speaking the cells of any species of wasp or bee are orientated in a more or less definitive way. It is true there are always divergences from the normal in one direction or another, the range of divergence being in some cases comparatively insignificant (scarcely exceeding 5°-10°), though in others exceeding 90°. Examples of bees building only erect or nearly erect cells are found in *Tetralonia malvae* Rossi, *Augochlora humeralis* Patton and *Nomia* amongst solitary

[1] In order to measure the volume of the cells of *Chalicodoma muraria* L. Fabre filled them with sand and then poured the latter into measured glass tubes. This method can be readily applied to free cells; but the measuring of the volume and the general dimensions of dependent cells and especially of autocoelous ones is often attended with great difficulty, chiefly because the successful opening of these cells (indispensable for their exact measurement) depends greatly on chance. I obtained the best results by filling the cells before opening them with gypsum or wax. The cast is then measured after the walls of the cell have been removed. There has not existed hitherto a uniform method of measurement and it is often difficult to decide what the figures given in a description of a cell mean: whether the whole cell or only the cavity.

bees and species of *Trigona* and *Bombus* amongst the social. Much more often, however, the cells are inclined downwards or horizontal, though, under certain conditions (at the ends of branches, thatched roofs, sometimes in the earth — *Xylocopa olivieri* Lep., etc.), inclined upwards. Inverted cells, on the contrary, are very rare in bees. Best known are the inverted queen cells of *Apis mellifera* L. and those of *Osmia simillima* Sm. (Packard, 1868). On the other hand this type of cell is very characteristic of social wasps.

The orientation of cells in either of the extreme positions (erect or inverted), which is possible owing to the capacity of bees and wasps to maintain themselves and work in almost any posture (including head downwards), has its advantages and drawbacks. Thus, when the cell is inverted it is necessarily protected from obstruction from above; and rubbish and refuse may be very readily removed from it during construction. On the other hand, the preparation of provisions and feeding of the larvae in such cells requires special adaptations (both must be fastened to the bottom or to the longitudinal walls, or to both). In erect cells the relations are inverse, requiring different adaptations which are actually found in each case: e. g. the arch-like canals of *Tetralonia malvae* Rossi, the cavities around the cells of *Augochlora* and *Nomia*, etc. It must be noted that the question of the extremes divergence possible in the orientation of cells has been very little investigated. Thus, for instance, I succeeded in inducing *Ceratina callosa* F. to orientate its cells in a position almost diametrically opposed to the usual one (the erect).

The type of orientation is, moreover, connected with the nesting-site chosen. This connection is quite obvious in the overwhelming majority of lodger and carpenter bees. When they choose a narrow ready-made cavity, sufficient only for the recepcion of but one row of cells; when they excavate such a nest-canal themselves along the grain of wood, these bees automatically determine the position of the cells which they have built. The direction of the longitudinal axis of the cavity occupied and of that of the cells then mostly quite or nearly coincide. A cell whose orientation is determined by the nature of the nesting-site may be called an allothesal [1].

[1] θεσις, position.

In contrast to this digger-bees, mason bees and occasionally other bees determine the degree of inclination of the cell for themselves since they choose a nesting-site which permits any orientation of the cells. These are consequently autothesal cells. Either type may have any position, i. e., they may be erect, inclined downwards, horizontal, inclined upwards or inverted. These examples of different types of orientation, above mentioned, are mainly found in autothesal cells.

The method of provisioning cells is also partly connected with their orientation. The importance of cleanliness in this connection has already been mentioned (see the protection of the cells from obstruction) and will be discussed further on (see the life of the larvae).

*The Order in which the Cells are constructed.* The way in which the different walls of the same cell are constructed has been considered above; I intend to dwell here on the order in which different cells are constructed. If we observe the order in which the construction of the cells proceeds we find in some cases a regular routine; after the construction one cell is quite finished, a second is begun, and there is no return to the first one. Here we have, therefore, two separate series of actions following the one after the other; the cells are independent one from another not only structurally but, so to speak, psychologically as well. In other cases, however, several cells are built more or less simultaneously; before the construction of one cell is really finished, that of the following, sometimes of several cells, begins while work at the first cell may be recontinued at intervals. When construction proceeds in this fashion, generally speaking, a series of cells rather than a single one is being built. The routine mentioned is here, therefore, greatly disturbed, and the psychological independence of the cells is wanting while their structural independence is preserved only in part, more rarely entirely and sometimes, as we shall see, is quite lost. The cells of the first kind we shall call consecutive, those of the second serial (simultaneously build). The former are typical of almost all solitary bees and wasps and the latter are built almost exclusively by the social species.

According to the degree in which the routine of the construction of the serial cells is disturbed, they may be divided into three groups:

*

semi honey-comb, true honey-comb and composite, according as the construction of the cells is only partly, or quite simultaneous or, thirdly, when there is no distinction at all is made between different cells. In the first case a new cell is begun only when the preceeding is finished but for its cover. Theoretically, one could have a species in which no cover was built, so it is more convenient to characterize these serial cells, as those in which the final stages of the work (provisioning, laying of the egg, building of the cover) take place only when the following cell is more or less finished. Among the solitary bees, these «simultaneously built» cells are found according to Smith (1901), in *Augochlora humeralis* Patton and *Halictus quadricinctus* F. (*quadristrigatus* Latr.), according to Verhoeff, and apparently, according to the author's observations, in *H. calceatus* Scop. They appear to occur sometimes also in those solitary wasps, which actually attended to several cells simultaneously, e. g. in *Odynerus tropicalis* Sauss. observed by Roubaud (1916).

In the case of «true honey-comb» cells the building of new ones begins when the construction of the longitudinal walls of the preceeding cells is not yet finished and the latter is resumed from time to time. Here also other work (provisioning) is done in connection with several cells simultaneously. The true honey-comb cells appear to be peculiar to the social wasps and the majority of social bees (except the humble-bees). The most frequent interruptions in the regular routine of the work on the cells can be observed if one follows the actions of a single individual when founding a community — as can be done most readily in *Polistes gallicus* L. and with less convenience in other social wasps (*Vespa crabro* L., etc.).

In the case of those simultaneously built cells, which are not distinct frum one another, there is not only no definite routine for each separate cell, but the cells are never structurally distinct here, therefore one almost continuous complex is formed — the *composite* cell. In my opinion the peculiar cell of humble bees in which contrary to the usual habits of bees several individuals are brought up simultaneously is of this nature (pl. VI, fig. 28; pl. X, fig. 48).

As can be seen from the preceeding examples the simultaneously built cells may be dependent or independent, most often the latter.

Divergences of another kind are observed in the order in which

the separate cells of the same nest are built. The building of some cells is always preceeded by the construction of the corresponding galleries, while the other cells of the nest are situated along the galleries already completed (sometimes there is only one gallery). Thus, for instance *Andrena bimaculata* K., under favourable circumstances, after having excavated the first gallery and built the first cell at its end and two others before it on the same gallery, excavates the second lateral gallery and builds at ist end a new cell, the fourth one, and again two more before it; the work is continued under the same system (fig. 59). Such a method results in a great economy of time and labour. Even though the actual routine adopted has considerable complications. The cell whose construction preceeded that of the gallery at the end of which it is situated, is generally the main cell; the remaining one or more cells are adventitious cells. The division of cells into main and adventitious cells is obviously only possible in dependent and especially autocoelous cells. Hence the most characteristic adventitious cells are to be met with in the digger and carpenter bees.

Summarizing all that has been said above, the following chief types of the cells may be recognised.

According to their destination .....
- inhabited ...
  - male cells,
  - female cells,
  - worker cells;
- uninhabited.
  - protective cells,
  - storage cells,
  - supplementary cells.

According to their shape .....
- elongate,
- shortened,
- homomorphous,
- heteromorphous,
- bilaterally-symmetrical,
- radially-symmetrical,
- asymmetrical,
- dependent (allomorphous),
- independent (automorphous) cells.

According to the construction of the cells-walls.....
- holotichal,
- hemitichal,
- allotichal,
- autotichal,
- heterotichal.

According to the origin of the building material.....
- endostoechal,
- ectostoechal cells.

According to the character of the cell-cavity.....
- allocoelous,
- autocoelous,
- moderately capacious,
- narrow,
- wide cells.

According to their orientation.....
- erect,
- inclined downwards,
- horizontal,
- inclined upwards,
- inverted,
- allothesal,
- autothesal.

According to the order of construction.....
- consecutive,
- serial.....
  - semi honey-comb,
  - true honey-comb,
  - composite;
- main,
- adventitious.

This classification of cells has not previously been developed completely, though some particulars of it have been published before. Thus I already had occasion to write (1911, 1917) about independent and dependent, erect and horizontal cells, cells built of materials found close at hand or of material brought in from outside. In the literature mention is often made of other kinds of cells, e. g. bomb-like, inflated cells, barrel-like, pouch-like, cup cells, half cells, barrel cells, etc.

Some of these names indicate details in the shape of the cells, while others emphasize peculiarities in their external aspect, when examined together with their vestibule (such at any rate are the «pouch-like», and perhaps barrel-like cells); several of these terms are insufficiently clear and precise.

## The Provision of Food.

Solitary bees provide their cells entirely or mainly with food of vegetable origin — nectar and pollen, often apparently mixed with the secretions of their salivary glands. Social bees behave in a similar way. In the latter the «royal jelly» injected into the cell in feeding up of the queen of *Apis mellifera* L. may replace the pollen entirely. The nectar supplies the carbohydrates and the pollen or salivary food

the albuminous substances or proteins. Wasps, on the contrary, nearly always feed their young on animal food — insects of different kinds and ages and spiders. The only exceptions are the solitary wasps of the family *Masaridae* and the social ones of the genus *Nectarina*, which provide their larvae with honey food. Honey is also sometimes found in the cells of *Polistes* but there it is stored not so much for the large larvae or adult wasps as for the new-born young (Wheeler, 1908; Rau, 1928).

In visiting flowers for the collection of provisions, bees usually have more or less definite predilections. In this respect they have been divided (Robertson and others) into monotropic, oligotropic and polytropic. The first type collect only from one definite plant or from a few closely related species. Thus, for instance, *Andrena florea* F. visits only the flowers of *Bryonia alba; Macropis labiata* F. only those of *Lysimachia vulgaris; Emphor bombiformis* Cress., only those of *Hibiscus lasiocarpus; Tetralonia malvae* Rossi, those of either *Lavatera thuringiana* L. or *Althaea officinalis* L., etc. Oligotropic bees visit several different plants, e. g., *Meliturga clavicornis* Latr., *Melilotus officinalis, Medicago sativa; Melitta leporina* Pz., *Medicago falcata, Melilotus officinalis, Trifolium montanum.* The polytropic species have no special preferences and visit many different plants according to their opportunities. Such bees are *Osmia rufa* L., *Anthophora acervorum* L., *Xylocopa valga* Gerst. and apparently all social bees. The great majority of solitary bees are, however, more mono or oligotropic [1].

In the actual method of visiting flowers different bees have different habits: some «wallow» in the flower (*Dasypoda*, *Panurgus*), others run about on it (*Megachile*), while several simply suck up the nectar and brush off the pollen with their feet or scrape it off with their mandibles; others, again, bite through the corolla (*Xylocopa*).

No species, however, appears to confine itself to gathering from a

[1] In deciding to which of these groups a bee ought to be referred, it is the collecting of provisions that is important and not the mere visiting of flowers for its own feeding.

According to the degree of preference shown by the bee for the one plant or another in gathering provisions for the nest, Ihering has made a further distinction between the main and the accessory flowers.

single flower only, but having visited one flower they proceed to others either on foot (*Ceratina callosa* F.) or on the wing (*Anthophora acervorum* L.). Thus the collection of one load consists, as a rule, of a number of similar actions repeated several times. The wasps, on the contrary, normally gather each load of (animal) provisions in one act.

Only as an exception, doubtless of a primitive character, the pollen and nectar gathered for the nest is swallowed and so transported inside the body of the bee, in its crop where they are, of course, mixed together (*Prosopis*). As a rule, however, only the nectar is transported in this way; to it, either in the process of gathering, or in the course of transport or regurgitation, is added, probably, the secretions from the salivary glands which act on the nectar to form honey.

Leaving out of consideration this exception (*Prosopis*), the pollen, when collected, is transported to the nest by the bee on the surface of its body, where it fills the space between special collector-hairs, usually dense and long, and adapted to this purpose, or, more rarely in special «baskets», i. e., bare areas of the integument, fringed with fine hairs. The collector-hairs are situated on different areas of the body or on the legs — chiefly the hind ones. Of the former kind are the tufts (the thoracic fringe, *fimbria thoracis*) at the back of the sternum on the sides of the intermediate segment in *Andrena*, the brushes beneath the abdomen in the *Megachilinae*, or those on the sides and part of the dorsal surface of the abdomen in *Systropha* (fig. 30). On the legs the collector-hairs, arranged in brushes or pencils, are found on all joints of the hind legs, but most often on the tibiae and metatarsi (pl. VII, fig. 31). Sometimes the collector-hairs may occupy several different areas on the same bee; thus in *Andrena*, besides the tufts already mentioned, there are some (floculi) on the trochanters and brushes on the tibiae and metatarsi. The pollen-baskets, which are characteristic of social bees and almost absent in the solitary ones (though present in *Euglossa*, *Canephorula*), occur exclusively on the outer surface of the hind tibiae [1]. The remarkable moth *Pronuba yuccasella* Riley, on the contrary, does not attach the pollen which it has gathered and made into a lump, to itself, but uses its mouthparts to hold it in flight.

[1] The occurrence of the pollinia of orchids on the head of *Ceratina* and *Apis* is apparently accidental.

The Mexican wasps (*Nectarina*) already mentioned appear to behave in the same way. Other wasps also hold their animal booty with their feet or mandibles and only *Oxybelus* has the queer habit of transfixing its victim on its sting and letting it trail along behind.

According to the way in which the pollen is packed for transport one can distinguish (according to Friese and others) loose and compact loads. In the first case, most common in the solitary bees, the bee keeps the pollen in its natural state, while in the second, characteristic especially of the social, but also several solitary bees (*Melitta, Macropis, Meliturga, Rhophites, Eucera*) it moistens the pollen with honey by means of its proboscis and feet (pl. VII, fig. 33). The amount of honey added often varies in the same bee, doubtless in dependence on the same general causes that influence the secretion of nectar by plants (temperature, moisture of the air, the our of the day) as well as on stage which cell-provisioning has reached. This will be discussed latter. In *Meliturga clavicornis* Latr. I sometimes observed the pollen-mass attached all the way round its hind tibia like a muff (fig. 32) and so juicy that it shone and smeared the edges of the wings if it touched them. Since we know the kind of food stored in this bee's cell, we are bound to conclude, that it conveys on its hind tibia not only the pollen but also all the honey, which it accumulates in the cell — a method of transport directly opposite to that of *Prosopis*.

When a sufficient load of provisions has been accumulated, the bee returns to its nest and deposits it in a cell. In this respect one can notice an essential difference between social and solitary bees. The latter, as far as it is certainly known, under normal conditions only provide the inhabited cells with food, while the former deposit it also in the storage-cells. There are, however, statements (Friese, 1905, 1914), that some solitary bees, *Lithurgus dentipes* Sm. and *Xylocopa caerulea* F., also store food in cells, where afterwards no eggs are laid, and that they avail themselves of these stores in bad weather, when they are building new cells. These observations are however too briefly recorded and certain necessary details are lacking. According to my recent investigations, *Lithurgus* and *Xylocopa* do not provide their cells «for case of need» and statements just mentioned have another explanation (Malyshev, 1930, 1931). Owing to the same uniform method of storage, solitary bees never keep honey apart from

pollen, as the social bees often do, but always mix them. In the first load at least (except *Prosopis* ?) pollen predominates or even composes the whole load.

According to whether the labour of storing the cell is continuous or interrupted, one may distinguish (according to Rouband and others) two modes of providing the cell with food: mass and progressive provisioning. The first of these methods consists in conveying more or less uninterruptedly all the food necessary for the development of one larva, regardless of what it needs at the actual moment. As far as we know, all solitary and some of the social bees (*Melipona, Trigona*) and the vast majority of solitary wasps, act in this way (except *Allodape* ?). In progressive-provisioning, the food is carried to the cell from time to time, more or less in relation to the daily need of the larva which is being fed. This behaviour is found in the rest of the social bees (*Bombus, Apis*), some of the solitary wasps (*Monedula, Bembix, Odynerus tropicalis* and others) and all the social wasps. Behaviour somewhat resembling progressive-provisioning may be seen when (as is rare in solitary bees), their collection is sometimes interrupted by the bee to add to the longitudinal walls of the cell, as in *Chalicodoma* and *Anthidium latreillei* Lep., according to Réaumur and Ferton (1914).

Entering into the nest with its load of provision, the bee turns round and backs into the cell, where it brushes off the pollen with its feet; certain bees (*Eriades florisomnis* L.) actually turn round outside the nest, so that they enter it backwards. When the pollen has been deposited on the bottom or floor of the cell, the bee turns round, so that she may eject the honey from her crop. The species of *Osmia* which nest is narrow galleries have to leave the nest for this purpose. The load deposited in the nest is usually carefully mixed with the nectar. This, of course, is done only when the honey is brought simultaneously with the pollen; otherwise the bee immediately proceeds to his work.

In order to provision a cell adequately the bee has to make several journeys to gather pollen and nectar from flowers and to deposit them in the cell. The number of these journeys can sometimes be determined from the layers in the pollen or from differences in its colour, which result from several loads being superimposed on one

another. In this way one can deduce that *Osmia rufa* L. returns with a load of pollen at least five or six times to complete the provisioning of one cell. G. Müller (1885) has ascertained by careful weighting that a single load of *Dasypoda plumipes* weighs 0.0383-0.0435 gr. and that the food for one cell consists of 6-8 loads of pollen, besides the nectar (weight up to 0.3577 gr.). The more liquid provisions (*Colletes cunicularius* L., *Anthophora acervorum* L.) probably necessitate more frequent journeys. The last load deposited in the cell usually consists mainly of honey. By way of comparison, it may be mentioned that wasps often store a cell in one load only.

The amount of provisions stored in a cell is related to the size of the individual for which it is destined in the same way as the size of the cell cavity (see above). Consequently the quantity of provisions in female cells is often much greater than in those of the males. But in many cases (especially in the digger-bees) it depends on various secondary factors (which will be indicated later on) besides on the bee's activities.

According to the species and genus of the bee, very different amounts of honey and pollen respectively are found in the provisions. When honey obviously predominates, the provisions are more or less liquid, honey-like (*Prosopis*, *Colletes*, *Anthophora*, *Megachile rotundata* F., *Trachusa serratulae* Pz.); while the presence of pollen in greater quantities renders them either viscous and dough-like (*Andrena*, *Halictus*, *Melitta*, *Meliturga*, *Osmia adunca* Pz. and many others) or non-viscous and gruel-like (*Tetralonia malvae* Rossi, *Xylocopa valga* Gerst. [1]). Of the same consistency also is the «royal-jelly» stored up in the queen cells of the hive-bees *Apis mellifera* L. When there is much more pollen than honey the food is dry and friable (*Lithurgus fuscipennis* Lep., *Osmia solskyi* Mor., *Eriades truncorum* L., etc.). The mixing of the two constituents of the provisions is often incomplete; thus in *Osmia rufa* L. the rather big lump of bee-bread is often thickly covered all over with dry pollen and in *Tetralonia malvae* Rossi, the gruel-like provisions are covered by a thin layer of transparent honey (pl. XV, fig. 68; pl. V, fig. 16).

When the provisions are honey-like or pollen-like the bee does not

[1] See p. 249 for changes in the consistency of the food, which happen without the intervention of the bee.

attempt to mould them into any special shape. The food simply fills up the posterior half of the cell. Only the upper surface of the food-mass may be oblique or may show traces of the food having flown in or of having been brushed in. Sometimes the gruel-like or dough-like provisions also are equally without shape (*Tetralonia malvae* Rossi, *Osmia leucomelana* K., *Megachile bombycina* Rad., *Anthidium florentinum* F., *Eriades campanularum* K., etc.). None of these give any shape to the food-mass (pl. XI, fig. 52, 53, 55). In many cases, however, the dough-like provisions are given some shape only partly dependent on that of the cell. According to the perfection of the form given to the provisions one can distinguish «half-moulded» and «fully-moulded» provisions. The contours of the former differ from those of the cell not only on their upper or anterior side but also to a considerable extent laterally; the remaining surfaces are fastened to the walls of the cell or at least touch them (pl. V, fig. 18, 20; pl. IX, fig. 42; pl. XI, fig. 54). This method of preparing provisions is characteristic of *Melitta* (*M. leporina* Pz.), *Panurginus* (*P. labiatus* Ev.) and apparently of the majority of species of *Osmia* (*O. adunca* Pz., *O. cyanea* F., *O. rufa* L., *O. tridentata* Duf. et Perr., etc.).

When the provisions are fully-moulded only a small area of the surface of the food-mass is fastened or touches to the cell-walls; usually this area is reduced to a minimum. Thus in *Andrena* (usually), *Halictus* (always), *Augochlora, Panurgus* and *Meliturga* the provisions look like either a roundish, more or less flattened loaf resting on the floor or seldom (*Augochlora*) on the bottom of the cell; only the underside of the food-mass or even only a part of it touches the cell-walls (pl. VIII, fig. 36, 38, 39; pl. VI, fig. 22). The provisions of *Andrena bimaculata* K., of *Systropha* and *Rhophites* have the shape of a regular sphere which is laid freely on the floor of the cell (pl. IX, fig. 40, 41); in *Xylocopa valga* Gerst. the hugeloaf, occupying almost the whole length of the cell, touches the floor and sides of the cell only with the anterior-lateral and posterior parts of its surface (fig. 25 and 46); the «cakes» of *Ceratina callosa* L., are fastened to the cell-partition corresponding to the floor by only a very small part of one of its larger surfaces (fig. 26 and 69). The provisions of *Dasypoda plumipes* Pz. look like a short three-sided pyramid stand-

ing on three conical legs, of which two are anterior and one posterior (fig. 23, 44 and 45). As a rule, however, fully-moulded, as well as half-moulded or unmoulded provisions are arranged symmetrically.

The moulding of the provisions when it occurs may be started at the very beginning of the provisioning of the cell; thus in *Rhophites canus* Ev. even the first load of pollen is deposited in a roundish though as yet angular lump. In other cases the fully-moulded provisions lie at first for a longer or shorter time in a shapeless mass, being either pollen-like (*Andrena ovina* Kl.) or thick gruel-like (*Xylocopa valga* Gerst.). *Dasypoda plumipes* Pz. according to Müller, whose statement I have not been able to confirm, a short time before the provisioning of the cell is completed, covers the roundish lump of food with moist sand; each time a new load is added the sand is removed.

The provisions however prepared not unfrequently undergo various changes apart from the action of the bee. Some of these changes are normal, necessary and useful in the economy of the bee, while others injurious and fatal to them. Of the first type is the liquefaction of the provisions which I have detected in many solitary bees (notably in the typical digger-bees) and which is well known to play an important part in *Apis mellifera* L. during hibernation. This is due to the hygroscopic properties of honey which at cool temperatures, about 10° C. for instance, readily absorbs moisture from the air so that the consistency of the provisions changes and it may increase twofold or more in bulk. This property of honey explains the appearance of a transparent non-viscous liquid round the loaf of *Andrena ovina* Kl. and further that of small drops on the walls of the cells of *Andrena florea* F., *Halictus sexcinctus* F., etc. (pl. VIII, fig. 37, 38); the same phenomenon probably explains the fact that the eggs of *Panurginus labiatus* Ev. are found on small lumps of provisions while semi-adult larvae occur on larger ones (compare fig. 42 and 43). This proves, in this case, that the provisions increase up to a certain amount more rapidly than the larva which feeds upon them is able to consume them.

Further in the cells with honey-like food there is usually a precipitation dividing it into two (*Colletes cunicularius*) or three (*Anthophora acervorum*) layers.

Either in conjunction with these processes or independently, the provisions may begin to turn sour. The first to discover this (in the cells of *Colletes succinctus* L.) was Mayet, but it appears to occur also in the cells of all bees which store honey-like, diluted gruel-like or dough-like provisions. It is revealed by the appearance of gas in the food-mass and by a characteristic «sour» smell. Considering that this phenomenon constantly occurs in the cells of such a bee as *Colletes cunicularius* L. and that it is harmless to the larva, it must be considered normal, at least for solitary bees and sometimes even necessary for the sucessful development of the larvae.

Others but abnormal processes are the drying up of the provisions and the growth of mould upon them. If they do not become very dry, the larva only eats them more slowly, but if the drying up proceeds more rapidly, they may become altogether uneatable. Thus if the juicy cake of *Ceratina callosa* F. be pressed against the wall of the cell, it dries rapidly, and five or six days later the young larva perishes. The appearance of mould also usually kills the larva.

If we now consider the relation between the consistency and moulding of the provisions to the orientation of the cell, it is evident that they are not much connected. Provisions of any consistency —e. g. honey-like, gruel-like, dough-like or pollen-like—, may be stored in cells with any type of orientation. It is sufficient to note that the cells of *Prosopis* which are provided with honey-like food, may be either horizontally or even strongly inclined upwards, but they seem nevertheless to retain their liquid contents. It is not surprising, therefore, that more viscous food can be stored in inverted cells, e. g. the gruel-like provisions of the queen cells of *Apis mellifera* L. or the more solid provisions of different species of *Megachile*, *Osmia*, etc. stored in nests in thatched roofs etc. There is thus no direct connection between the consistency of the provisions and the orientation of the cell. The case is different, however, when the provisions are of a type which alters afterwards. Whatever the consistency given to them by the bee, whether honey-like, gruel-like or dough-like, they are always stored in obliquely descending or in erect cells. This is quite natural for the transparent liquor which accumulates has great fluidity and its surface (e. g. in the inclined cells of *Andrena ovina* Kl.) is always horizontal.

Unmoulded and partially moulded provisions are also found in cells with different orientations; food masses of the latter type are most often met with in more or less inclined cells. The unattached but skillfully moulded provisions of certain bees (*Systropha*, *Rhophites*, *Dasypoda*) are, however peculiar to horizontal cells. A bee cannot of course prepare this moulded food-mass in an inverted cell — even in one strongly inclined upwards; at least some contrivance would be needed to hold the food in place. In any case there is another reason why provisions of this kind would not be prepared in either erect cells or in ones sloping upwards to any great degree, viz., the lack of space at the bottom of the cell would be likely to interfere with the movements necessary for the elaborate moulding of the provisions. Thus the cell of *Dasypoda* (*D. plumipes* Pz.) is one of the most spacious, while that of *Tetralonia* (*T. malvae* Rossi) which stores unmoulded provisions, is actually one of the narrowest.

A much closer connection may be observed between the way of preparing the food and the construction of the cell-walls. In the first place, digger-wasps (in the broadest sense) which store provision very different from those of bees, do not build any special cell-walls with the exception of the barrier at the entrance. On the contrary these walls are very characteristic of digger and other bees, the only remarkable exception to this rule being *Dasypoda*, which builds heterotichal cells, like those of the digger-wasps. One gains the impression that the building of special walls to the cells (besides the lid) has been necessary in order to retain honey when stored in the ground. In particular, the honey-like and gruel-like provisions are always kept in autotichal cells, whose longitudinal walls are made water-tight (*Prosopis, Colletes, Tetralonia, Anthophora, Chalicodoma, Trachusa, Megachile rotundata* F., etc.). Any exceptions to this rule are probably only accidental aberrations, as, for instance, when an unusual place is chosen for the nest (e. g. *Osmia bidentata* Mor. in a bulrush instead of cells of *Anthophora pubescens* F.) or when the cells are irregularly constructed, being, for instance, heterotichal instead of autotichal. In this case the provisions usually dry up, become porous and the larvae die. Pollen-like provisions on the contrary, are usually stored in cells whose sides at least have no special walls (*Eriades truncorum* L., *Lithurgus fuscipennis* Lep.). Dough-like provisions may be

kept in cells of any type. Often these cells have special water-tight walls (*Andrena, Halictus, Panurgus, Melitta, Megachile bombycina* Rad., etc.). When such walls are not constructed, as not rarely is the case, the great skill shown in moulding the provisions becomes increasingly important.

Though moulded food-masses are sometimes stored in autotichal cells with water-tight walls, e. g. in *Andrena bimaculata* K. and amongst the bees mentioned above, the provisions in these cases usually, sooner or later become more or less liquid by the natural process already described. When the cell-walls are hygroscopic in spite of their special construction (*Systropha, Rhophites*), the skillfully moulded dough-like provisions are always kept from touching the walls of the cells — so that even liquefaction, if it takes place, does not lead to contact. Thus *Osmia tridentata* Duf. et Perr. and often other *Osmia* species also keep the roundish lump of semiliquid provisions from touching the hygroscopic cell-walls by a thin layer of dry pollen. We have already described the «cakes» of *Ceratina* and *Xylocopa*, the spherical food-masses of *Systropha* and *Rhophites* and the «loaf» of *Dasypoda* supported on three legs. In all of these bees the surface of contact between the hygroscopic walls of the cell and the provisions, is reduced to a minimum. The way in which the larvae eat the carefully moulded provisions also confirms, as we shall see later, the supposition this is a device to isolate the food from the walls of the cell. We may, therefore, make a generalization, at least with regard to digger and carpenter bees, that the less care they bestow on the construction of the walls of the cell, the greater the skill shown in moulding the provisions. The moulding of the food-mass in cells with hygroscopic walls has, of course other functions, partly in connection with their subsequent liquefaction, partly with the method of laying the egg. I will only mention here that the free surface which absorbes the moisture from the air is increased by the shape given to the provisions.

## The Laying of the Egg.

All definite evidence we have at present indicates that solitary bees lay one egg only in each inhabited cell. Packard's statement

(1867) that *Ceratina dupla* Say., lays one or more eggs in a cell, appears to be an error, perhaps resulting from confusing the eggs of the parasite with those of the host (see Graenicher, 1905). Again, Gutbier (1916) has suggested that *Lithurgus fuscipennis* Lep. lays more than one egg per cell; but my special investigation (1930) has shown that the bee, too, follows the usual rule (pl. VI, fig. 27). Among solitary bees the only exception to this habit appears to occur in certain South African species of *Allodape*, summarily recorded by Brauns (Wheeler, 1925). In these species one may say that normal cells are not constructed and numerous larvae are brought up together in more or less close contact (see above p. 228). The social bees also usually lay one egg only in each cell. The queen humble bees (*Bombus*) which lay a dozen or even more eggs (Sladen, 1912) in their peculiar cell are the only real exceptions (fig. 28 and 48), for though the honey-bee, *Apis mellifera*, sometimes lays several (two to seven) eggs in a cell, this always indicates some abnormality in the hive (illness, a drone-laying queen, a very young queen, deficiency of nurse-bees, etc.). In the wasps *Eumenes tinctor* Christ. also, according to the observations of Roubaud (1916) in South Africa, lays several eggs in one cell, but only in periods of drought, when prey is scarce. Further the cuckoo-bees (*Stelis, Melecta*), ruby wasps (*Chrysididae*) and a few other parasites sometimes lay several eggs in the cells of their host (Malyshev, 1911). In these cases, except in the humble-bees (and *Allodape ?*), only one individual successfully completes its development. Thus with the exception of humble-bees, of parasites and of abnormal behaviour in particular individuals, it is a strict rule that bees lay only one egg in each cell.

Further in solitary bees the egg seems always to be laid after the provisioning of the cell has been completed; only *Lythurgus* (*L. fuscipennis* Lep.) laies its eggs during the process of securing the provisions (pl. XI, fig. 56). The majority of the solitary wasps and part of the social bees (*Melipona, Trigona*) behave in the same way. The remainder of the social bees (*Apis* and commonly *Bombus*), and all the social and some of the solitary wasps (*Sphegidae* of the genera *Monedula, Stizus*, and all *Diploptera*, i. e. families *Eumenidae, Vespidae* and *Masaridae*) lay their eggs in empty cells. In social species division of labour has, of course an important influence for some members of the

colony (usually one in each nest) lay the eggs while others bring the provisions, so that one would not except these acts to follow one another in the same regular order. Still it is interesting to note that the so-called laying workers in the hives of the honey-bee readily lay eggs in cells provided with pollen, thus following the same rule as the solitary bees and social bees of the tropics already mentioned. On the other hand the female of the humble-bee, when she is independently constructing the first cell, begins by storing provisions and then lays the eggs. Of the humble-bees observed by Sladen (1912), a few species which retain the most primitive type of behaviour (*Bombus ruderatus* F., *B. hortorum* L.) always lay their eggs on a layer of provisions in the first cell. This layer, is however, insufficient for the complete development of the larvae and the mother continues to feed them in small instalments. Thus the laying of eggs is performed during the process of securing the provisions. Those solitary wasps which lay their eggs on the food stored, also act as a rule in the same way. Finally there is some reason to suppose that wasps which now lay eggs before any food has been collected, formerly laid them during this process or immediately after it (Malyshev, 1911) and that consequently the habit of providing the cell with food before the eggs are laid must be considered as the more primitive. This will, however, be reconsidered later.

When the egg is laid after the food has been prepared, it may be attached either to the wall of the cell, or to the provisions, or simultaneously to either. Thus in *Colletes*, as Mayet (1875) discovered in *C. succinctus* L., the egg is glued with one end to that longitudinal wall which owing to the inclination of the cell, serves as the ceiling, the opposite end of the egg projecting freely into the cell-cavity; it may happen sometimes that the egg touches the provisions (in *C. compacta* Cress., according to Smith), but this is probably accidental. In *C. cunicularius* L. I found that the egg is fastened to the ceiling by its anterior end (fig. 15 and 35). *Ceratina callosa* F. and *C. cyanea* K. also fasten the egg by the posterior end near the bottom of the cell to the longitudinal wall of the cell, but to the one which forms the floor. At the same time it lies under the provisions on which its anterior end rests. In the rest of the solitary bees, as known, the egg is always laid on the provisions (in *Lithurgus* within the egg chamber).

Here we may distinguish between three methods. In the first the egg rests on the provisions with only the posterior end submerged, appears to be the most usual position for the egg. It may be adopted when the food is pollen-like, often when it is dough-like and quite unmoulded (*Megachile bombycina* Rad.), partially moulded (*Panurginus labiatus* Ev., fig. 42) or fully moulded (*Andrena*, *Halictus*, etc.). The second method is employed by bees, whose eggs are strongly bent like a bow, so that the two ends rest on the food, one end at least being inserted into the provisions, which may be either honey-like (*Anthophora acervorum* L., fig. 17), gruel-like (*Tetralonia malvae* Rossi, fig. 16) or dough-like and skilfully moulded (*Halictus major* Nyl.). The third method adopted by bees having a rod-like or slightly bent egg consists in allowing the whole or the greater part of the underside of the egg to be covered by the provisions. (*Prosopis*, fig. 14, 34) or to lie freely on the surface (*Xylocopa*, *Systropha*, *Rhophites*, *Dasypoda*). It is clear from these instances that the third method may be employed when the provisions are either honey-like or dough-like and moulded with the utmost skill. It is remarkable that *Ceramius lusitanicus* Klug (a wasp of the family of the *Masaridae*), which lays its egg like other allied wasps on the wall of the cell before the cell is provisioned, yet according to Ferton (1901) it moulds the dough-like honey-food into the shape of a retort, on to whose short neck-like appendix the egg is afterwards transferred. Numerous though not fully verified observations suggest that the workers of *Apis mellifera* L. are able to transfer the eggs laid by the queen from one place to another.

Wherever the egg of a solitary bee may be laid the ventral side of the egg is always directed towards the provisions. This appears to be a necessary condition for the successful hatching and development of the larva, at any rate if the provisions are honey-like or have a similar consistency. The way in which the egg-shell is thrown off (see later on) also proves this. This must be considered as another reason for giving a shape to the provisions in cells provided with a watertight bottom and longitudinal walls. Indeed, if the digger-bees laid their eggs on unmoulded dough-like provisions, then if liquefaction took place subsequently, the egg would be immersed (if fastened to the food) in the increased volume of liquid food or even if the egg floated owing to the surface tension, it would lie on one side owing to its

crescent-like shape. Either way it would be fatal. To avoid this danger, various measures are adopted. Thus in *Tetralonia malvae* Rossi, for instance, the shell of the bow-shaped egg has smooth shiny ends while the rest of its surface is rough, so that it always rests with the ends only on the food. Even if one of the ends is lifted up and then dropped, the egg will again assume its usual position. The egg of *Andrena ovina* Kl., on the other hand rests on a solid «loaf» of provisions which is gradually almost entirely submerged by the liquifying honey, the end of the egg which projects into the air, gradually reclining on to the surface of the provisions (pl. VIII, fig. 37). The glueing of the egg to the wall of the cell above the provisions has already been mentioned in *Colletes*. Thus when the circumstances require it some measure is always taken to prevent the egg from «drowning».

Finally it may be noted that small drops of a transparent liquid are sometimes seen on the eggs of certain bees (*Halictus major* Nyl.). It is difficult, however, to tell whether the drops are deposited by the bee on purpose, or whether they are the result of accidentally smearing the egg-shell with honey which subsequently liquefies.

## The Sealing up of the Cell.

After having provisioned the cell and laid its egg the solitary bee definitely closes it up [1]. Following the habit widely spread amongst solitary bees the cell is sealed up immediately after the egg is laid (except *Lithurgus* and *Allodape;* see above). Sometimes the bee (*Chalicodoma pyrenaica* Lep.) even brings the material for sealing the cell and the last load of provisions, on which it deposits the egg, simultaneously and then inmediately closes the cell (Fabre). Only exceptionally is the sealing up of the cell retarded. Thus, according to Verhoeff's observations on *Halictus quadricinctus* F., several completely stored but still unsealed cells may be seen at the same time. Though the definite closure of an inhabited cell takes place after the egg is deposited, yet the cover itself may be prepared previously at

[1] The provisory closing of the cells, and cells which are left open, have already been mentioned.

the same time as the other walls. A remarkable case of this nature is seen in *Colletes;* here the cover prepared beforehand is the so-called membranous threshold, which I discovered first in the mouths of the cells of *C. cunicularius* L. and later in those of other species (*C. constrictus* Pérez, *C. daviesanus* Sm.). When the cell is completely provisioned the *Colletes* detaches the loosely fastened anterior border of the threshold; owing to its elasticity this structure rises and shuts the entrance of the cell. The bee then has only to cement the borders of the cover with saliva, which hardens to a silky membrane. This is done immediately. In *Prosopis*, also, one can sometimes detect only the mere rudiments of such a threshold, but this does not serve as a cover.

In other cases, as has been mentioned, the construction of the cell-cover is quite a separate piece of work from that of the other cell-walls. When the mouth of the cell has taken shape the cover is fitted into it; or is simply made in the place corresponding to the entrance of the cell which it defines anteriorly.

The cover is usually built of materials which do not differ essentially from those used for the other cell-walls; or to speak more accurately, the same material is used to construct the cell-cover as for the other autotichal parts. To this rule the cell-covers of most digger-bees are in peculiar exception. In this case the material is taken from the nearest walls of the vestibule of the cell or from the rim of its mouth which, after the cell has been closed, is found to be considerably damaged, apparently in this way (*Panurgus calcaratus* Scop., *Anthophora acervorum* L.). From this habit as well as from direct observation, it can be seen that the cover consists of the same building material, which served for the construction of the outer (earthen) layer of the cell itself. Thus the inner lining of the cell does not, as a rule, extend to the cover. The species of *Anthophora,* however, are remarkable exceptions, for the cell-cover is polished on the inside also. Wesenberg-Lund (1889-1890) supposes that the bee (*Anthophora parietina* F.) accomplishes this by putting its proboscis through the central opening in the cover and so spreads the hardening secretion over its inner surface. I can scarcely, however, accept this explanation, for the secretion is derived in reality from the anal end of the bee (at least in *Anthophora acervorum* L. according to my

observations); it is the tail of the bee which is introduced into the aperture (Malyshev, 1928).

Cell-covers may thus be distinguished according to their permeability with respect to moisture into permeable (*Andrena, Halictus, Melitta, Panurginus, Osmia rufa* L., etc.) and impermeable (*Prosopis, Colletes, Anthophora, Ceratina, Xylocopa, Chalicodoma*, etc.). It seems evident that the hermetic closure of the cells would best protect their contents from unfavourable external influences, especially excessive dryness or moisture. The existence of permeable cell-covers may, perhaps be explained in one of two ways; either the bees that construct them are unable to reach inside to polish them (though even then they might polish the outside !), or the permeability of the cover is part of their plan of building. Whatever the immediate cause of this property of the cover may be, there is no doubt that its permeability must exercise an essential influence on the contents of the cell, especially on the consistence of the provisions, so that the water-permeability of the cover, at least, in digger-bees of necessity must be compensated for by the choice of nesting-site, the orientation of the cell, the structure of the other walls, the mode of provisioning, etc. This is what we actually find, e. g. a moulded food-mass is found in cells with water-tight walls and bottom (compare, the account of the position of the egg).

One can further distinguish between loose and compact covers. The former consist of uncemented separate particles heaped up in deliberate disorder at the entrance of the cell. Such covers are seldom observed in bees; they are especially typical of the species of *Halictus* (*H. calceatus* Scop., *H. major* Nyl., pl. VIII, fig. 39, etc.), the wool-collecting species of *Anthidium* (*A. florentinum* F., etc.) and sometimes, species of *Ceratina* (*C. callosa* F. in some nests). Compact covers are the type most usual in bees. They consist either of particles arranged in a definite manner, usually cemented together, or of entire pieces of various substances (*Colletes, Andrena, Megachile*, etc.).

A special type of compact cover can be distinguished, the «spiral cover» in which the particles are regularly arranged in a more or less regular spiral, usually quite obvious when seem from the inside of the cell. Sometimes this spiral may be put together rather roughly (*Pa-*

*nurginus, Dasypoda*), but in other cases with remarkable accuracy (*Rhophites, Systropha, Melitta*). The spiral usually has 4-5 whirls (pl. IX, fig. 40, 41). Sometimes the cover consists of two parts, the inner spiral, the outer compact and smoothed, but unpolished (*Meliturga, Anthophora, Rhophites*). The spiral cover is mainly found amongst the digger, more rarely amongst the carpenter-bees (*Xylocopa, Anthophora furcata* Pz.).

Further compact covers are not infrequently simple, the constituent particles being arranged not spirally but in some more simple manner (e. g. in a series of separate arcs) or continuously (*Osmia, Chalicodoma, Ceratina*). Sometimes the cover consists of larger particles deposited one after the other each of them filling the whole width of the cell-entrance (e. g. the majority of the species of *Megachile*). As far as I know, however, simple compact covers are found chiefly amongst mason and lodger bees and only occasionally amongst other types (seldom amongst digger-bees — *Colletes*).

Having closed the cell, some bees moreover forbid access to it by making a barricade [1]. This is a heap of separate particles, always left uncemented and piled without order, which either partly or entirely fills up the gallery leading to the cell. Thus no hard and fast line can be drawn between loosely made covers and a barricade (especially in *Halictus major* Nyl.) except, perhaps, that they are not made in quite the same situation in the nest. It might, therefore, be more correct to consider that *Halictus* and similar forms do not construct a cover at all, but only block up the cell with a barricade. Since the barricade is not a part of the cell itself, the former may be made of material very different from that of the cell. Thus it may be endostoechal while the especial cell-walls are built of ectostoechal materials (*Osmia parvula* Duf. et Perr.), or, though the materials may be endostoechal like the cell-walls, yet they may be taken from the walls of the nest and not secreted by the bee itself (*Colletes cunicularius* L.). More often, however, there is no such sharp distinction between the building material of the barricade and that of the cell-walls (mostly digger-bees, *Megachile bombycina* Rad., etc.).

When the barricade is built with endostoechal material, the latter

[1] *Lithurgus* makes this barricade immediately after the provisioning of the cell has been completed.

is usually removed from one part of the nest where consequently a more or less deep excavation is formed. Although the bee often uses this hole in the construction of the nest cell, it is certain that it acts similarly when closing the last cell, though the last-made excavation cannot be used (*Colletes cunicularius* L., *Tetralonia malvae* Rossi). After having closed the completely stored cell, a solitary bee normally leaves it for good (exceptions will be considered later).

## The Number of Cells in the Nest.

Very few solitary bees (and even these, it appears not invariably) construct nests of one cell only. The nest of *Osmia papaveris* Latr. is the best known instance of this kind; but even this species as Latreille definitely records sometimes builds two cells in a nest. The first of these cells according to the terminology, I wish to establish, is the main one and the second the adventitious one. Nests with only one cell and of the simplest plan are, on the contrary, characteristic of many wasps (*Scoliidae*, the majority of the *Pompilidae*, many *Sphegidae*, a few *Eumenidae*).

Solitary bees build as a rule several cells in one nest (many-celled nests). The number of cells is determined partly by external conditions (the size of the cavity, hardness of the substratum, etc.) but also by internal factors such as the innate building instinct of the bee and her age. The number of cells in one nest with the digger and mason-bees, is not usually very large, — 5 to 6, seldom more (up to 10 in *Andrena bimaculata* K., 15 *Chalicodoma muraria* F.). In lodger- and carpenter-bees the average number may be higher though the maximum remains the same (up to 15 in *Osmia tricornis* Latr., 17 in *Ceratina callosa* F. and 19 in *Xylocopa valga* Gerst.). These remarks refer, of course, to solitary nests built by one individual; nests, due to several individuals (composite nests) and particularly those of social bees, generally consist of many cells, often several hundreds or even thousands.

## The Arrangement of the Cells.

We have already said that each cell may be completely isolated from all the others (one-celled nests) though this is not characteristic of bees but only of the lower wasps. Much more often, however, particularly in bees there is some definite arrangement of the cells. The first method is to keep each cell separate (nests with separate cells). The second method leads to what may be called nests with connected cells.

The connection between the cells of one nest may be simple or complex. In the first case all the cells are connected with each other in one way, in the second in two or several ways. In the digger-bees, and among the bees apparently in this group only, the cells of one nest are usually all connected with each other by the main gallery, common to all of them, and special lateral galleries for each separate cell. This arrangement of the cells may be called ramifying. We can further distinguish between progressive, regressive and stationary methods of ramifying according to the variation in the depth or length of the main gallery as the number of cells increases, i. e. whether it gets deeper, less deep or remains the same [1]. There are, however, instances of a ramifying arrangement of cells, when the connection between the construction of the main canal and the increase of the number of cells is not so clear and definite (e. g. in *Halictus major* Nyl.); this may be called the dispersive method of ramification (pl. XIV, fig. 64). Each of these four ways of arranging the cells is characteristic of this or that species and often genus of digger-bees. Thus *Colletes cunicularius* L. for instance arranges its cells constantly in the regressive ramifying method, while progressive ramification is characteristic of the galleries of the genus *Systropha* (pl. XIII; pl. IV).

Not infrequently one finds clockwise and anti-clockwise systems of ramification but this distinction is not so important as the fourfold classification already made, for individuals of the same species differ in their choice of these methods, e. g. *Colletes cunicularius* L. may

[1] See p. 217 with regard to the construction of the galleries.

arrange the cell-galleries either clockwise or in the reverse way. Sometimes the directions of the arrangement of the cells on the horizontal plane are not constant in the same nest (*Systropha, Halictus sexcinctus* Latr.). Hence it is clear, besides the vertical or horizontal directions of the arrangement of the cells, the angles which they make with one another in the horizontal and vertical planes may also vary. In certain cases this angle remains remarkably constant for the cells of the same nest (*Colletes cunicularius* L.).

In the lodger-bees and some carpenter-bees the cells are usually connected only by a single common gallery or, if there is more than one gallery, they are not constructed by the bee herself and therefore, have the same significance for her. This may be called the linear arrangement, and as a direct consequence of this method, the cells are usually related to one another in a further way, viz. the bottom of one cell is closely applied to the cover of the preceding cell which was built just before it; it may more or less coalesce with it (coalescent linear arrangement; pl. XV, fig. 68). More rarely the cells, though arranged in the same way are constructed at some (usually small) distance from one another (the separate linear arrangement, sometimes observed in *Osmia parvula* Duf. et Perr., *Ceratina callosa* F., fig. 69, etc.).

Certain digger-bees and more frequently carpenter-bees have a habit of arranging their cells in a way that might be called 'ramifying-linear plan, for certain features of each method are here combined. The nest as a whole has ramifying galleries, but in each gallery the cells follow the linear arrangement. Here again we can distinguish two further systems. In the one type the cells adjoining the common nest-gallery or common lateral gallery (both made by the builder itself) are arranged so that the longitudinal axes of neighbouring cells form a more or less considerable angle (usually acute) with one another. This is the primary ramifying-linear arrangement (*Andrena bimaculata* K.). In the other type the longitudinal axes of adjacent cells lie in a more or less straight line. This is the secondary ramifying-linear method (*Xylocopa valga* Gerst., *Anthophora acervorum* L., etc.). (See figs. 59 and 11.)

The mason-bees have a characteristic habit of building their cells side by side with the longitudinal walls in contact. This produces a

sort of compact mass of the cells, — corporeal arrangement. The cells may be disposed irregularly in more or less compact clusters (heaped-up arrangement), as for instance in *Chalicodoma pyrenaica* Lep.; or form on the contrary a regular complex, either the tops and bottoms of the cells being all on the same level, or the cells being arranged to form a half-cylinder or other curved surface (honeycomb-like arrangement). Such complexes or «honey-combs» are almost peculiar to the social bees, and are rare amongst solitary species (*Halictus* in part, *Augochlora*, *Anthophora balneorum* Lep., *Anthidium laterale* Latr., pl. XV, fig. 70).

Sometimes the connection between the cells, which are arranged essentially as in honey-combs, is so complete, that the longitudinal walls of the cells disappear entirely. In this way, at least in my opinion, arose the peculiar «cells» (really honey-combs of coalescent cells) of the humble bees (*Bombus*).

The cells may also be arranged in ways intermediate between the honeycomb-like and the linear or ramifying methods. Thus, the cells of *Osmia coerulescens* L. (fig. 67) for instance, which occupy a common nest-cavity are often connected with each other not only end to end (i. e. in the linear way) but also by their longitudinal walls, as in the honeycomb type. This may be called the linear method with many rows. In *Osmia jucunda* Sm., the cells, without regard to the sizes and form of the cavity (as in the typical honeycomb-like arrangement), are often linearly connected with each other. This is the «linear cluster» arrangement.

It is remarkable that the regular honeycomb-like arrangement of the cells much more rarely grades into the ramifying than it does into the linear system. This rare intermediate type is seen in those nests in which the cells are regularly connected by their sides and are enclosed in a more or less common cavity, the so-called breeding chamber, which represents, at least in origin, the result of the coalescence of several much shortened lateral galleries. In these nests the cells may be said to be arranged in chambers. This method is characteristic of some species of *Halictus* (*H. calceatus* Scop., fig. 65, *H. quadricinctus* F.), *Augochlora* (*A. humeralis* Patton) and a few other bees which build «earth honeycomb».

## The Distribution of the Sexes in the Nest.

This question may be considered as an only special feature of the way in which the cells are arranged, viz. the male and female (and worker-cells in the social-bees), but it has also a special interest of its own. The main source of information concerning the distribution of the sexes in the nests of solitary bees is the remarkable and extended investigations of Fabre, who came to the following final conclusions:

1. When the sexes are of a different size and require different amounts of food, the bee lays its eggs in two series; first a series of females, then one of males. If the size of the sexes is the same, such a division may be made, but it is less definite.

2. This division of the egg-laying is not made, if there is insufficient room to lay all the eggs on one nest. In this case the eggs are laid at intervals beginning with the females and ending with the males.

3. When the egg emerges from the oviduct, it is as yet of no definite sex. Only at the moment of being laid or a little earlier is it subjected to the influence on which its sex depends.

4. To secure for the larva the requisite amount of space and quantity of food, the mother controls the sex of the egg laid. According to the space available it lays either a male or female-producing egg: in a word, the sex of the egg depends on the will of the bee.

5. If circumstances demand it, the order in which the sexes are distributed may be reversed, i. e. begin with the males, or finally the whole batch may include one sex only.

6. The wasps, too, have the same faculty, at least those species in which the sexes are of different sizes, requiring, therefore, different quantities of food. The mother must know the sex of the egg she is about to lay, and so arranges that each larva receives its due portion.

7. When ever sexes are of different sizes, any insect which provides housing and food for its progeny must also control

the sex of the egg, in order to supply the needs of its offspring without fail.

Of these conclusions only the third is uncertain; for the same result might be obtained if the egg when leaving the ovipositor was male, and became female only after fertilisation (Dzierzon). There are also other facts which disagree with Fabre's statement.

The most common or, at least, the most obvious type of distribution is seen when, in one cavity, female cells are built first and later, in the anterior part of the nest, male ones, a phenomenon which Verhoeff (1891) has called proterothesis of the males, even making it a general law, admitting of no exceptions. The same author was the first to distinguish between male, female and bisexual nests, i. e. those containing only males, only females or both sexes together. The nests of the social bees, at least at a certain stage in their construction, may thus be called three-caste nests.

The tendency to distribute the sexes in a nest in a definite way must, of course, be most marked in bees which excavate their own nest cavity or construct the cells in more or less open places, so that the size of the cell is not influenced by external factors, in other words, in digger, carpenter, and mason bees (as far as they do not use the old nests of their own species). Unfortunately at present almost nothing is known of the distribution of sexes in digger-bees. Indirect evidence (the amount of provisions) suggest that *Andrena bimaculata* K., a species which arranges its cells on the ramifying-linear plan, puts males in the main cells and females in the adventitious. For instance in a nest of nine completed cells (fig. 59) the sexes appeared to be distributed as follows:

| Cells: | I | II | III | IV | V | VI | VII | VIII | IX |
|---|---|---|---|---|---|---|---|---|---|
| Individuals: | ♂ | ♀ | ♀ | ♂ | ♀ | ♀ | ♂ | ♀ | ♀ |

Similarly in the nests of *Halictus quadricinctus* F., with the cells grouped in a breeding chamber, Verhoeff (1897) states the male cells are built first. This does not agree either with Fabre's first two conclusions or with Verhoeff's theory of proterothesis of the males.

Our knowledge of the distribution of the sexes in carpenter-bees

is fuller though far from sufficiently complete. The following are some instances:

*a)* in linear nests,

*Osmia tridentata* Duf. et Perr. (according to Fabre)

1) ♀ ♀ ♂ ♀ ♂ ♀ ♂ ♂ ♀ ♀ ♀ ♀ ♂ ♀ ♂.

2) ♀ ♀ ♂ ♀ ♂ ♀ ♀ ♀ ♀ ♀ ♂ ♀.

*Osmia parvula* Duf. et Perr. (according to Hoeppner)

♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♂ ♂ ♂ ♂ ♂ ♂ ♂ ♂ ♂ ♂ ♂.

*Ceratina callosa* F. (according to the author)

1) ♂ ♂ + ♀ ♂ ♂ ♀ ♂ ♀ →

2) ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ + + + →

*b)* in linear-branched nests,

*Xylocopa valga* Gerst. (according to the author)

♀ ♂ ♂ ♀ ♀ ♀ ♀ ♂ ♂ ♀ ♀ ♀ ♂ ♂

In the mason-bees the species best known in this respect, *Chalicodoma muraria* F., when building a new nest in a suitable place «begins laying female producing eggs and concludes with male producing ones, there being an unmixed row of each sex» (Fabre). Moreover in the coalescent honey-comb of *Bombus*, males and females (less frequently males and workers or one sex only) often develop together, the males being situated at the sides of the group and the females in the middle (Sladen). The lodger-bees have a general tendency to put females in the earlier cells and males in the later, but even more characteristic is their remarkably developed ability to control the sex of the egg according to the space available. If in the cases considered above the bees constructed a male or female cell as a result of internal influences, which we cannot explain, the lodger-bees (and others when they avail themselves of old cells) must often construct the cell for a particular sex under compulsion of the environment (i. e. consideration of space). This influence may be so great as to disturb the usual order of the oviposition and even to invert it. Fabre's investigation of the distribution of the sexes in *Osmia tricornis* Latr. leaves no doubt as to this. We shall have further occasion

to dwell on the significance of this habit, especially in lodger-bees (including *Chalicodoma*, etc.), in connection with the behaviour of young bees in leaving the nest.

## The closing of the Nest.

When the construction of the cells of the nest is completed, the bee closes it with the nest-cover [1]. The bees of the genus *Ceratina* and *Xylocopa* are nevertheless the exceptions. According to Verhoeff, *Ceratina coerulea* Vill. (= *cyanea* K.), does not shut the completed nest with a special barrier. I succeeded, however, in ascertaining that *C. callosa* F. is capable of closing the nest, though it only does so exceptionally. Thus the normal absence of a cover to the nests of *Ceratina* and *Xylocopa* is in reality connected with certain peculiarities in their habits and especially with the tendency to work on one nest to exhaustion, so that the bee is forced to sit at the entrance of the nest, which it defends as well as it can (with the mandibles, aromatic saliva, sting, etc.). Thus instead of the usual mechanical protection there is a «living barrier» as in the case of the social bees. *Lithurgus* (*L. juscipennis* Lep.) does not close the nest also.

The nest-cover is only very rarely built from inside the nest, so that the bee imprisons itself in the nest. Nevertheless, *Andrena ovina* Kl. and, apparently, those species of *Halictus* which build earth honeycombs (*H. calceatus* Scop., etc.) appear to do this. Usually the nest-cover is constructed from without, and the bee leaves the nest for ever.

Nest covers may be divided into loose, compact and mixed types. The first kind is made of uncemented particles, more or less tightly fitted together. It looks like a barricade placed in the entrance of the nest and is found chiefly, though not always, amongst the digger-bees (*Andrena, Melitta, Tetralonia*, etc.) and carpenter-bees (*Anthophora furcata* Pz., at least commonly, and *Ceratina callosa* F.). The nest-covers of the second type are made by cementing the particles together, and most frecuently consist of a series of transverse partitions separated from each other and the last cell by empty spaces. The

[1] Temporary closing of the nest has already been mentioned.

compact type of nest cover is most characteristic of lodger-bees (genera *Prosopis, Osmia, Eriades,* etc.) and of some of the mason-bees (*Chalicodoma muraria* F., *Osmia globicola* Stadl., etc.). The third kind of cover consists of both loose and compact structures (the barricade, partitions, tampon, etc.) sometimes also connected by a system of cavities. It may be found in various bees. Of this type, for instance, is the nest-cover of *Anthophora acervorum* L., *Osmia leucomelaena* K. and *Anthidium septemdentatum* Lep.

The materials of which the loose nest-cover is made has the same origin and nature as to the barricades closing the individual cells, the only difference being, at least when the nest is closed from without, that the material for the nest-cover is taken from the anterior part of the nest where a new gallery will never be made; this gives rise to a large recess on one side of the burrow or subspherical chamber (*Anthophora acervorum* L., *Tetralonia malvae* Rossi). The loose type of nest-cover is also often partly made of material derived from the tumulus (*Colletes cunicularius* L., *Andrena bimaculata* K., *Tetralonia malvae* Rossi) and, apparently, from other superstructures, e. g. the entrance tube (*Anthophora parietina* F.) [1]. The loose part of the mixed type of nest-cover are also often made of the same as the barricades of the individual cells (if such a barricade is present), but there are exceptions; thus *Osmia parvula* Duf. et Perr. makes the barricades between the cells of shavings of the pith of the stem occupied, while the loose part of the nest-cover is composed of fragments of plant-stems, grains of sand, etc. Part of the nest-cover is often uncemented even when there is no barricade whatever in front of the individual cells (*Anthidium septemdentatum* Lep.). As far as is known, however, it appears, that when building material for the loose type of nest-cover, or for the loose part of the mixed type, is brought in from outside, special walls of the cell are also ectostoechal.

Compact nest-covers, and the compact parts of those of the mixed type, are always of the same nature as the special walls of the cells. In other words, if the cells are made of endostoechal material the compact nest-cover is built of the same material, and vice versa: so

[1] According to Wesenberg-Lund (1889-1890) and Nielsen (1902) the material of the entrance tube is also used *(Anthophora)* for building the earthen walls of the cells: this, however, requires verification.

that a nest whose cell-walls are of ectostoechal material is closed by an ectostoechal cover. The few exceptions result from the function of the nest-cover in keeping out intruders. Thus pieces of quartz, snail-shells, etc., either large (*Megachile lefebvrei* Lep., as big as the head or even the whole bee) or small and arranged in one or several rows, are often inserted amongst the carefully shaped cells (Ferton, 1897). *Anthidium florentinum* F., which usually builds cells of vegetable fibre (sometimes of the pappus of compositae) seals up the nest with green mastic, while in *Megachile lefebvrei* Lep., the hard inclusions in the cell-cover are cemented with green mastic, the cells themselves being made of mineral dust mixed with the bee's saliva [1]. In other cases the last cell, either unaltered or specially modified, serves as a nestcover, at the bottom of which there may even be deposited a load of pollen (*Anthophora acervorum* L., *A. parietina* F., *Megachile picicornis* F. Mor.).

The nest-cover is usually internal, i. e. is inside the nest either at the very entrance (*Osmia rufa* L., *O. adunca* Latr., *Eriades, Megachile centuncularis* L., *Anthidium florentinum* F., etc.). In other cases the nest cover is somewhat intermediate in position, being partly inside the nest and often overlapping the edges of the entrance hole (*Anthophora fulvitarsis* Brullé). Rarely there is a complete outer nest-cover, which is spread over the whole outside of the nest (*Chalicodoma muraria* F., etc.). Lastly, there may be a double nest-cover, when beside the inner or intermediate cover, there is also an outer one, differing in material and construction from the first. Thus *Osmia bicolor* Schrank, after having sealed up the mouth of the shell, which it uses for its nest, with green mastic, covers the whole shell with pine-needles and grass-stems piled, not in an haphazard way, but following a regular plan, so that a kind of hut is formed, as P. Huber (1824) was the first to point out in much detail.

A quite exceptional way of closing the nest is found according to Ferton in a few species of *Osmia,* which transport (by rolling or dragging) the whole nest to a new place. Thus *Osmia rufohirta* Latr., having sealed the shell occupied with green mastic, trans-

[1] This case reminds one of the habit of *Odynerus murarius* L. which builds the partitions between the cells of clay and the exterior part of the nest-cover of «wasp-paper».

fers it under a tuft oı grass or to some other safe place, and *O. fossoria* Pérez, after closing the nest (again an empty shell) with a mixture of vegetable cement and fragments of shells, digs in the neighbourhood a shallow pit in which it buries the nest.

After having completed its nest in one of these ways, the solitary bee not infrequently proceeds to construct a second, which, in distinction to the first or main one, may be called a adventitious nest.

## II. Classification of Nests.

To provide for their progeny bees build a great variety os nests [1]. In order to appreciate this variety more fully, the nests may be considered from several points of view and may be compared in their various aspects with one another. Part of this survey has already been made on the preceeding pages, and as a result we recognized the following types of nests:

| | |
|---|---|
| according to the population of the nests. | male nests,<br>female nests,<br>bisexual nests,<br>three-caste nests; |
| to the number of the cells. ..... | one-celled nests,<br>many-celled nests; |
| to the connection between the cells ... | nests with separate cells,<br>nests with connected cells; |
| to the order of construction..... | main nests,<br>adventitious nests; |
| to the number of nests combined into one structure by one builder ..... | simple nests,<br>combined nests; |
| to the number of builders. ..... | solitary nests,<br>composite nests: true colonial and social; |
| to the affinity of the builders..... | pure nests,<br>mixed nests. |

[1] Later on we shall see that in the solitary bees nests are sometimes, though very rarely, constructed for another purpose (cf. the life of the males).

To this list of distinctions must be added that subsisting between normal nests, such as we are dealing with the whole time, and abnormal nests, which form part of the subject of the following chapter.

Since all nests necessarily fall into one or other of the above divisions, the groups obtained in this way have all the same significance and do not provide a system of classification. Now our task is to attempt to elaborate a uniform system, which will enable us to define the relations of different bees'-nests (and also wasps'-nests) to one another with respect to their complexity and so obtain a deeper insight into their genetic relationship or evolution. Attempts in the literature to arrive at a natural classification of the nests of bees (and wasps) are all up to the present time purely tentative. Of the diverse and usually rather summary attempts of this kind, I regard as most important those of Graber (1877) and Verhoeff (1892), since they are based on a principle which is without doubt correct though applied in a very imperfect and often erroneous way [1].

Graber only distinguishes four types of wasp and bee nests. The first assemblage, a rather artificial group, is left without a name; it is described as follows: «Only a few of the solitary wasps have cells built by the mother for her individual offspring — cells without any connexion with one another.» Certain sand wasps and *Eumenes pomiformis* are given as examples of these «free builders» (Freibauern). He next points out how slight a connexion often exists between cells of similar construction. The next three «systems» receive a name but are loosely and somewhat erroneously defined: viz., branched (Zweigbau), linear (Reihenbau), and flat or honeycomb like (Flachen oder Wabenbau) constructions.

Verhoeff gives a more correct classification with more suitable descriptive terms.

[1] A little earlier Waterhouse (1864, p. 115) divided the nests of bees and wasps into three groups:

I. Nests formed in burrows in the ground, or in dead wood;

II. Isolated cells not deposited in such excavations, but merely attached to some foreign substance;

III. Groups of cells more or less closely united, not deposited in excavations or burrows, but either attached to some foreign substance, or to a nest-covering made by the insects. Here the form of the cell is commonly hexagonal.

*

1. One-celled constructions (Monocien: Greek, μονος, one, and οκιον, a room): each cell is connected with the exterior by one gallery (Stollen).

2. Linear constructions (Orthocien: Greek, ορθος, straight): numerous cells arranged in a line, one behind the other, all of them having the same exit-hole.

3. Branched constructions (Dendracien: Greek, δενδρον, a tree): many celled constructions having one main entrance and gallery into which the occupant of each cell can get by a branch gallery without disturbing the rest of the inhabitants:

*a*) Branched constructions with separate cells. The cells are situated far from one another and each of them is connected with the main gallery by a separate passage.

*b*) Branched constructions with close-lying cells. In consequence of being crowded together, the cells have lost their separate passages to the main gallery on which they therefore open directly.

4. Free constructions (Eleutherocien: Greek, ελευθερος, free). The cells (not consisting of galleries in clay, sand, stony ground, or in plant stems, branches of trees, or in wood) lie freely on slopes, rocks, walls, etc. Such constructions may be:

*a*) One-celled structures.

*b*) Many-celled structures.

5. Vaulted-constructions (Troglocien: Greek, τρογλη, a cave) For the most part there are no cells in the sense previously used. A comparatively large space may be occupied by numerous inhabitants. There is usually a cover made of extraneous matter. A subterranean or sub-aerial (*Bombus*) construction lying always concealed.

6. Honeycomb constructions (Melissocien: Greek, μελισσα, honey) of *Apis*. (Each group may be again divided into sub-groups according to the material used in the structure.

Subsequently Friese (1905, 1922) has indicated the following groups of bees' nests:

I. One-celled nests (sometimes as an exception in *Trachusa serratulae, Anthophora fulvitarsis*).

II. Many-celled nests:

1. Linear structures (Linienbauten) in the ground or in wood — found in *Colletes, Prosopis, Ceratina, Megachile*, etc.

2. Branched structures (Zweigbauten) in the ground — found in *Anthophora* and *Trachusa*.

3. Cluster-like structures (Traubenbauten) in the ground — in *Andrena*, *Dasypoda*, *Eucera*.

4. Fingershaped structures (Fingerbauten) only in wood, in *Lithurgus*.

5. Heaped-up structures (Haufenbauten) free on stones — in *Osmia*, *Chalicodoma*, etc.

6. Honeycomb structures (Wabenbauten) — in solitary bees found in *Halictus quadricinctus*.

7. Heaped-up structures (Haufenbauten) in the social bees — *Bombus*.

8. Honeycomb structures (Wabenbauten) in the social bees, *Apis*.

In 1911 on the basis of the concordance of criteria (the relation of the shape of the cells to the shape of the space they occupy, the distribution of the cells, the construction of the stoppers to cells and nests, etc.), I divided the nests of wasps and bees into four groups («types»), viz. one-celled, branched, linear and free nests, to which I gave definitions, which then appeared to me as essentially the most satisfactory and sufficiently correct in form [1]. In 1916 developing this view I presented it in a special paper devoted to the question of the classification of the nests of bees and wasps; but owing to the then existing conditions this was not published until five years later (1921). To the classification then worked out I still adhere, having introduced only a few alterations and additions.

The nests of bees and of other animals cannot be considered as

[1] Gutbier (1916), having not altogether understood my views on this subject, misjudged and rejected them, and proposed his own «Classification» of nests. This, however, is based on an incorrect principle (the morphological) the various criteria are not properly subordinated and are moreover unhappily chosen and quite insufficiently characterised. The result is that instead of one classification there are really two, and when these are combined, a third system is evolved. This latter system is not treated in detail by Gutbier and would prove exceedingly complicated and inconvenient in practice, if one were to deduce it logically from his premises. These facts compel me to reject Gutbier's classification. I have treated this subject in more detail on another occasion (1917).

self-sufficient, containing in themselves the means for their construction, as, for instance, is the case in living organisms or crystals. They are on the contrary the product of the activity of the builders. Bees' nests however, unlike our own structures, show the effects of heredity in every essential feature and often in many details. At their basis lies instinct as a hereditary mode of action, and this is their characteristic peculiarity. We may even say, that the creative element (whatever its nature may be) manifesting itself in the morphogenetic processes, in the actual formation of the organism, may project itself into the surrounding medium and manifest itself in a construction of the bee type. In its completed state (especially in *Apis*) such a structure is essentially something very like the skeleton (exoskeleton) of the insect. Unlike the chitinous integument it is indeed separated from the insect in space, but it nevertheless fulfils some vital function. Another fundamental feature of these structures is their direct connection with the substratum though the form of their connection may vary extremely. For this reason bees' nests must be considered as the result of two elements: the active creative skill (usually only instinct) and the passive or even resistant substratum. Hence it would be wrong to apply the morphological principle alone to the elaboration of a natural classification, and only the biological principle, i. e. skill in building or the mode of construction adopted, can serve as a basis for the discrimination of classes. From this point of view the classification of bees' and wasps' nests ought to be at the same time, at least in its essence, a classification of their instincts as well. This biological or rather psychological principle not only admits, but requires that nests, which are built by essentially different methods even if they are on the whole similar externally (morphologically), should be taxonomically distinguished.

The degree of development attained in the building instinct may be used to divide the nests into natural groups of different significance and is best expressed in the relation of these two elements, which in their interaction produce the nests, viz. of the instinct and the substratum. In extreme cases we observe such a predominance of one of these factors, that the participation of the other in the construction of the nest is carcely discernible or manifests itself in one respect only. Thus for instance the primitively built nest of the wasp

*Calicurgus annulatus* F. [1], according to Fabre's description, is almost entirely dependent on the substratum for the shape of the cell, its capacity, the orientation of the walls, the building material, etc. The skill in building is here shown almost exclusively in the choice of situation for the nest. The inverse is seen in the nests of the social bees, where we see that the cells are not subjected to such restrictions by the substratum; they are independent of it as regards their shape, their capacity, orientation, material, etc. The substratum serves them as a support only.

Thus the degree of skill in building (the method of working) attained may be estimated not by the examination of the process of building only, but by the results also. The latter way of obtaining the necessary data presents considerable practical advantages and may be commonly adopted, if certain precautions are taken, especially if sufficient information is available with regard not only to the nest of the particular species of builder, but also to the nests of allied species and to the substratum; in doubtfull cases the progress of the work itself has to be studied. Hence a morphological investigation of the nest should in the first place aim at establishing of the connection between morphological peculiarities on the one hand and the method of construction on the other. When once such a connection has been established for all, or at least for the fundamentally different methods of building, the morphological classification of nests can and must be combined with the psychological, the latter providing the only rational foundation. At the present time, as far as I can judge, such a synthesis may be effected to a considerable degree, even if not completely.

Of all the manifold relations between the substratum and skill in building, the most important for the classification of nests is that on which the other relations must depend. Such a dominant relation is that, which I have previously (1911) proposed as the chief criterion for the classification of nests of bees and wasps, viz. the relation of the shape of the cell to that of the space it occupies. In this way sufficient weight is given to the cell, which is the only constant and also the most important constituent part of a nest, for

[1] In the bees such simple nests do not occur.

the other adventitious or secondary parts (the tumulus, galleries, nest barrier, etc.) may be wanting in a normally built nest [1].

According to the criterion chosen, we have two kinds of cells and in conformity with this two main groups of nests, the dependent and independent. Their methods of construction differ widely: in dependent nests the cell is built by means of a gallery leading from the surface of the substratum usually directly to its mouth. Here the bees do not know, so to speak, how to construct a cell without preparing or at least making use of an already existing burrow. Hence a dependent nest is also odalous [2]. In independent nests, on the contrary the cells are built without such an intermediate gallery. These nests, therefore, are also anodalous. The former are characteristic of the digger-, carpenter- and lodger-bees and the latter of the mason-bees.

Between the two main groups thus defined intermediate groups are found — as is usual in nature. However the distinction between dependent and independent cells and consequently the corresponding types of nests has been sufficiently indicated in a previous paragraph. We must further mention those nests where both kinds of cells, the dependent and independent are found together. The best-known example of this is *Halictus quadricinctus* F., in which, according to Verhoeff, the bee builds first dependent, and then independent cells. Under these circumstances, Verhoeff sees the manifestation of a biogenetic law in the domain of instinct. Hence nests of this kind, where the building instinct finds, finally, its highest expresion, must be referred to the independent type [3]. In a completed state, at any rate, they do not differ in anything essential from independent nests and are moreover an example of a nest, whose method of construction cannot be discovered by one, who has not watched the work actually

[1] The more simple constructions, consisting of only one or several secondary parts, are the product of either the undirected display of energy (play) on the part of insufficiently mature builders, or on the contrary, of senile degeneration or lastly, of the influence of unfavourable external conditions. As such these constructions must not enter into the classification of normally completed nests.

[2] Greek, ὁδός — a way.

[3] As for instance the insects are divided according to the peculiarities of their wings, though all of them in the course of their development pass through a wing-less stage.

in progress. Nests in which the passage from the surface of the substratum does not lead directly to the mouth of the cell, but through a special widening (the hatching chamber) in whose walls lie the mouths of the cells still under construction (*Halictus calceatus* Scop.), also belong to the intermediate type. Finally we know that cells may be constructed in such wide cavities, that there is no question of a passage (or burrow) in the strict sense (*Osmia coerulescens* L., fig. 67, etc.). Thus the relations of the shape of the cell to the space occupied proves more reliable as the main criterion than the presence or absence or special development of the nest gallery.

There are four ways of building and provisioning dependent cells. In the first place there may be a completely isolated burrow, a mere hollow of which part is occupied by the cell; these may be distinguished as autodalous nests; or, secondly, there may be two parts, some lateral galleries and a main gallery common to several cells; these are heterodalous nests; or the cells are built without special galleries and with only a passage more or less common to all cells and leading directly to the mouth of the cell under construction; these are allodalous nests. Or, finally, one or several (the main and lateral) common galleries run before reaching the cells into a special cavity common to all of them, the hatching chamber; such are synodalous nests.

From the above comparison it may be seen how different are the methods on which each of the four groups of dependent nests are built. They differ moreover in the order of work, the way in which the cells are arranged and the choice of the situation for the nests.

Thus the building of an autodalous nest is preceded by the choice of a suitable site, then the gallery is prepared and, finally follows the work in connection with the building of the cell itself. Every individual in an autodalous nest is provided for in this order, at any rate, in the most complete case (apart from provisioning of the cell). Hence there is no connection between the cells of such a nest and from comparative data it may be concluded that none ever existed. Thus the autodalous nests not only in their construction but also in their origin are one-celled nests in the strict sense. Nests of this type are found in many solitary waps (between *Pompilidae*, *Sphegidae*, etc.), but not in the bees.

In the building of heterodalous nests the choice of a site is followed by the digging of the main and then the lateral gallery; after this comes the construction and closing of the cell. Between the building of the first and of the remaining cells, the first two activities (the choice of site and digging of the main gallery) are omitted and only the subsequent activities are repeated. Finally the whole structure is completed by the closing of the nest. Thus the general order of work presents a considerable variety and complexity. In compensation, however, for this complexity much less energy in comparison with the preceding type is required to provide, other conditions being equal, for the same number of individuals. Here, therefore, there is a connection between the cells, a connection which is seen in their «branched» arrangement. Hence heterodalous nests are also branched. Among the bees they appear to be peculiar to the digger-bees.

The order of work in building an allodalous nest reminds one of that observed in the preceding type, but differs in that special (lateral) galleries are not constructed at all. Only the activities preceding the construction of the first cell (viz. choice of site and preparation of a common gallery to the nest) and those following the last cell (the closing of the nest) set these two cells apart from the rest and complicate matters. At any rate the amount of energy spent on the building of such a nest (the number of cells being equal) is still less (not to mention the utilization of old chambers). The result is a generally linear (coalescent linear, separate linear, many-rowed linear) disposition of the cells and the allodalous nest may therefore also be called linear. Such nests are peculiar to lodger- and to some extent to carpenter-bees.

Finally, in the building of synodalous nests, after the main gallery and the lateral gallery, common to all cells, have been prepared, the construction of the hatching chamber is begun. This chamber undergoes some alteration (enlargement, etc.) before the construction (or in connection with the construction) of every succeding cell. The work, consequently, becomes more and more complicated; but the presence of a hatching chamber and the honeycomb-like arrangement of the cells, enables the builder to watch all the cells of the nest simultaneously and each of them separately. Hence the synodalous nest

are also chambered nests. They are found only in certain digger-bees (*Augochlora*, part of *Halictus*, — apparently *Nomia*, *Megalopta*, etc.), whose building instincts approach those to one of the higher groups.

The branched, linear and chambered nests, like all nests with connected cells, pass during their construction through the stage of one-celled nests. Some of these nests remain in this stage in the absence of sufficiently favourable conditions. Finally, as a rare exception, the connection between the cells of a nest, which in its other features is allied to the connected-celled nests, may be almost completely absent (*Osmia papaveris* Latr.). Yet such one celled nests must nevertheless be referred to the connected-cell type, if it can be proved from comparative data that in this case the absence of a connection is of secondary origin, i. e. that it has been lost, has dropped out. Therefore the gallery leading to this cell is not a separate one in the proper sense, but a common one along which the other cells are no longer constructed or only rarely (as in *O. papaveris* Latr.). As far as I know no difficulties arise in practice in deciding this question [1].

Besides the above mentioned branched and linear nests, we know of many-celled dependent nest in which the characters of both types are to a certain degree combined. Such nests have already been mentioned by Verhoeff (1892), who did not, however, assign them a separate place in his system. Yet they are not rare and are characteristic of certain digger-bees and of most carpenter-bees, so that they may be set apart as a special type, the parodalous nests. Such constructions are most obviously characterized by the way in which their cells are disposed; on the whole this way is linear branched, either of the first or of the second order (see Arrangement of the Cells, p. 261). Hence, their old designation, —linear— branched nests.

The sequence in which the cells are built is of the greatest importance in the division of independent nests into groups of the second

[1] There is a certain want of logic in this procedure, but at any rate no more than in referring the wingless ants to the order of the Hymenoptera and so forth. The bees belonging to the same group as *O. papaveris* build «many celled» nests which may even be linear. Moreover the cell of this *Osmia* (like that of other species) is provided on the inside with a special lining, which is generally not the case in one celled nests.

order (types). Here we have two very distinct types, which have already been mentioned (p. 239), viz. the consecutive and the serial cells consequently two types of nests may be recognized, consecutive-celled (new cell is built after the preceding one has been finished) and honeycomb (serial-celled) nests (several cells are built at the same time). Moreover, in nests of the first type the building material is apparently always brought from without, while in the honeycomb nests the inhabited cells are either endostechal (in the bees) or ectostechal (in the wasps). Finally consecutive-celled nests are built only by the solitary bees and honeycomb nests only by all the social bees (as well as the social wasps) and partly those of the solitary species, which in many ways approach them.

Let us now pass on to dividing the groups of the second order (types) into groups of the third order (subtypes).

The one-celled (autodalous) nests according the origin of the cavity employed from the choice of site are either allocoelous, when the cell is built in a ready-made cavity in the substratum (allocoelous cell), or autocoelous, when the cell-cavity is made by the builder itself (autocoelous cell).

Branched (heterodalous) nests are divided according to the direction in which the work is carried out and consequently the disposition of the cells into: *a*) progressive nests (pl. IV, fig. 8; pl. XIII, fig. 62, 63), when the main gallery is lengthened with the increase in the number of cells so that each new cell is at a greater distance from the surface of the substratum; *b*) stationary, when the lateral galleries proceed radially from the end of the main gallery, whose depth therefore does not vary with the number of cells built (figs. 9, 61); *c*) regressive nests, when the depth of the main gallery decreases as the number of cells in the nest increases, since each new cell is situated nearer the surface of the substratum than the preceding one and the bottom of the main gallery is therefore filled up (fig. 7); *d)* dispersed nests, when the change in the length of the main gallery is not correlated in any definite way with the arrangement of the cells, which are located sometimes nearer to, sometimes farther from the surface of the substratum (figs. 10, 64).

Linear (allodalous) nests must be divided according to the way in which the building-material is procured. Since the building-material

is obtained either inside the nest or brought in from outside, the nests are either endostechal or ectostechal (pl. XV, figs. 69 and 68).

The same criterion is applicable for the division of the linear-branched (parodalous) nests into: 1) linear-branched of the first kind with endostechal cells disposed as a rule in the first linear-blanched manner (pl. XII, fig. 59); 2) linear-branched of the second type with ectostechal cells (pl. XIV, fig. 66), and 3) linear-branched of the third type without any special (autotichal) cell-walls, neither endostechal nor ectostechal (*Lithurgus fuscipennis* Lep.), — both apparently always disposed in the secondary branched manner.

The chambered nests according to the orientation of the cells may be divided into horizontal with the cells nearly horizontal (fig. 65) and vertical — with the cells vertical.

The degree of development attained by the builders of consecutive anodalous nests in ability to connect their cells with each other provides us with a basis for classifying this type, firstly into cluster-like nests, if the ability is not manifested in a constant and definite way (heapedup arrangement of the cells); then into linear-cluster nests, if there appears the tendency to connect the cells in a linear-clustering way, and finally into pseudo-honeycomb nests, if the cells (consecutive) are connected in the honeycomb way. A complex of cells of the last named group strongly recalls a true honeycomb nest but differs from it in the order of building (see above) and therefore can only be called pseudo-honeycomb (pl. XV, fig. 70).

Honeycomb nests readily fall into three groups according to the way in which the building material is procured. In the first group the cells are built of material taken from the walls of the cavity (apart from saliva used as cement). Hence such nests are «derived». The use of the secretions of special glands (the wax glands) of the abdomen is a characteristic feature of the cells (of the inhabited ones at any rate) of the second group, which must therefore be called «secreted». Finally in the third group of honeycomb nests the building material of the cells is brought from without; these nests may therefore be called «collected».

The interrelations of all types of nests established above, both in

bees and to some extent in wasps, are clearly shown in the following scheme:

| | | |
|---|---|---|
| Dependent nests (odalous). | One celled nests s. st. (autodalous). | Allocoelous *(Calicurgus annulatus* F.). |
| | | Autocoelous *(Pompilus viaticus* Latr.). |
| | Branched (heterodalous) ..... | Progressive *(Systropha curvicornis* Ill.). |
| | | Stationary *(Andrena ovina* Kl.). |
| | | Regressive *(Colletes cunicularius* L.). |
| | | Dispersed *(Halictus sexcinctus* F.). |
| | Linear-branched (parodalous) .... | 1st Type *(Andrena bimaculata* K.). |
| | | 2nd Type (*Trachusa serratulae* Panz.). |
| | | 3rd Type *(Lithurgus fuscipennis* Lep.). |
| | Linear (allodalous). | Endostechal *(Ceratina callosa* F.). |
| | | Ectostechal *(Osmia bicornis* L.). |
| | Chambered-nests (synodalous) .... | Horizontal *(Halictus calceatus* Scop.). |
| | | Vertical *(Augochlora humeralis* Patton). |
| Independent nests (anodalous). | Consecutive-celled. | Cluster-like *(Chalicodoma pyrenaica* Lep.). |
| | | Linear-cluster *(Osmia jucunda* Sm.). |
| | | Pseudo-honeycomb nests *(Anthidium laterale* Latr.). |
| | Honeycomb nests (serial-celled) ... | «Derived» *(Halictus quadricinctus* F. ?). |
| | | «Secreted» *(Apis mellifera* L.). |
| | | «Collected» *(Vespa).* |

The application of the criteria of the above system to individual cases, i. e. the determination of the correct place of a particular nest, is not frequently attended by great difficulties. The description of nests in the literature are often incomplete, various details, which would disclose the method of building being lacking. At any rate in order correctly to understand the construction of the nest, the old method must be improved. The present classification at least puts the most important questions on the subject, questions to which the reply allows of such an understanding.

In conclusion, I wish to point out that though the classification, as already mentioned, refers for the most part to the nests of bees, yet it is largely available for those of wasps as well. At first glance this may appear a strange coincidence, but it can be easily understood in view of the generally admitted opinion that the bees have originated from the wasps. This explains the similarity in the work of both. As the higher members of each family are specialized into smaller groups, the nests of the wasps gradually diverge from those of the

bees. Thus for instance, the true one celled and «collected» nests appear to be found only among the wasps, while «derived», chambered-nests and «secreted» nests occur only in the bees. Moreover the construction of the cells (autotichal and heterotichal) in branched nests shows an almost constant distinction between the nests of bees and wasps. The data necessary for the final division of the whole system in this way are still, however, lacking.

## III. **Old Age.**

The transition to the construction of adventitious nests usually indicates in solitary bees the beginning of the fourth and last period of their life — old age.

Much less frequently this period begins a little earlier, during the construction of the main nest (*Ceratina callosa* F., in part). On the other hand the lodger-bees, which necessarily adapt their activity to the space available, are not seldom compelled, as we know, to construct a succession of adventitious nests, of which only the last-built may bear traces of senility.

Nests built in the course of old age are distinguished mainly by the lack of the completeness and regularity observed in those constructed during maturity. This difference may be observable in various parts of the construction, which may be so little co-ordinated that the very reason for building a nest may appear lost. Thus, for instance, in senile nests the structure of the tumulus may alter beyond recognition (*Colletes cunicularius* L.). The nest gallery may be made either too shallow or too deep (*Ceratina callosa* F., *Augochlora humeralis* Patton). The transverse partitions dividing up the nest gallery into a series of cells may be placed at an excessive distance from one another (*Osmia rufa* L.) or may, in certain cases, instead of the usual «double partitions» form complexes of a higher order, — triple, quadruple or even more (*Ceratina callosa* F.). Again, instead of main cells, which are alone characteristic of the normal nest, adventitious cells may be built (*Andrena ovina* Kl.). The cells may be provided either with an excessive quantity of food (*Xylocopa valga* Gerst.), or,

as happens more frequently, with so little that there is far from sufficient for a single larva. Often no egg at all is laid on these provisions. Sometimes in cells which would normally be inhabited neither eggs nor even provisions are deposited (*Osmia tricornis* Latr., *O. rufa* L.). Generally in such cases the number of provisioned cells is very small, not much more than two, but it may also happen that the bee carefully closes a nest where it has not laid a single egg or even built anything whatsoever. «Being born for work, it must die working. When the ovaries are exhausted, it dissipates its remaining energy in useless work, — partitions, barriers or the collecting of unwanted pollen. The little animal machine cannot remain inactive even when there is nothing more left to do. It continues working in order to spend its remaining strength in aimless labour», — says Fabre of the old age of *Osmia tricornis* Latr.

These facts show that the bee continues to perform in its old age essentially the same actions as in its maturity. The chief difference consists mainly in the omission of certain links out of a chain of actions, which should succeed one another in a definite series. It is the same familiar series of activities, with the order unchanged and without additions, but only with such gaps in it that sometimes the very reason of the work is destroyed.

A very different phenomenon, however, may also be observed in the old age of bees. It may happen that they now perform actions they never did in their maturity or only when external influences disturbed the normal course of their lives. I refer here to attacks made upon the nest of others, attacks partaking not only of the character of theft but even of assault and even at times attaining epidemic frequency. Under these conditions everything is robbed, — the nesting-site, building material, provisions and eggs. Part of what has been stolen is destroyed, while what can be made use of is applied to their own work. Fabre's investigations of *Osmia tricornis* Latr. during the period when its work is finished, given a vivid picture of the havoc made amongst the nests by individuals that had previously worked side by side, sometimes destroying even their own previously built nests. Having destroyed the nest-cover and one or two cells, the bee removes the debris to the outside and begins to work afresh on her own, modelling partitions, conveying provisions, laying eggs, etc.

All this is done not because of any lack of room, since unoccupied tubes were still available. There was evidently a deeper cause — the senile degeneration of instinct already mentioned. Some authors have described theft and robbery among solitary bees, without mentioning at what period in the bee's life the observations were made. So for instance *Trachusa serratulae* Panz. according to Adlerz. These observations are so like those already described that the effects of old age must be seen here too. By interrupting for 24 hours the work of some individuals of *Chalicodoma pyrenaica* Lep., Fabre was able to induce them to attack the cells of other individuals and sometimes even sted their own which had been previously completed. Some of the individuals experimented on, however, proceeded immediately to the peaceful construction of new cells. Thus the results appeared contradictory and unfortunately there are no indications of any connection between this and the age of the bees.

Whatever may be the interpretation of the phenomena previously described, theft and robbery, as far as is known at present, are observed only when bees are living in close proximity, i. e., in colonies or associations. Thus with *Apis mellifera* L., the tendency to steal appears mainly when the possibility of collecting in nature has ceased, when theft may sometimes attain to extraordinary dimensions («slaughter»). The difficulty of getting naturally the material necessary for the construction and provisioning of cells may also lead to robbery. Lastly, mutual robbery amongst bees of one species, which on the whole nests independently in the normal manner, cannot but be considered as an evidence of some degree of affinity with the cuckoo-bees.

Besides building abnormal nests and making inroads upon the nests of other individuals, solitary bees sometimes behave in old age in quite a different way, more beneficial to the species. In this case, the bee, having finished building its cells, remains in the nest (usually the main one, less frequently the adventitious) and protects it as well as it can from the intrusions of small robbers and parasites, or such harmful influences as mould. Certain species of *Halictus* behave in this way (*Halictus quadricinctus* F., *H. calceatus* Scop.); after concluding the construction of their cells, they remain in the hatching chamber and keep their earthen «honeycombs» in a condition of perfect

tidiness. The same habit is probably found in *Augochlora humeralis* Patton. Further, in some cases a special (so to speack secondary) hatching chamber, serving apparently also as a dwelling for the aged builder which now only guards the nest (*Nomia ruficornis* Spin., *Xylocopa olivieri* Lep.), is excavated round the completed cells. But the young progeny may also be watched in a finished nest unprovided with a hatching chamber. Thus *Ceratina callosa* F., after building its linear nest, does not usually construct either a nest or a cell barrier, but sits between the entrance and the outermost of her offspring with her head turned towards it as if waiting for the completion of its development. If the mother *Ceratina* dies prematurely, her last unprotected young one usually also perishes. Something like this must be supposed to occur in *Allodape,* and perhaps in *Xylocopa* (*Xylocopa valga* Gerst.).

As a result, in some if not all of the species mentioned in the last paragraph, a new phenomenon appears, rather unexpected in the life of solitary bees, viz., the meeting of the mother bee with her young when adult. Such a «contact» between two generations undoubtedly played a very important part in the origin of social life among bees and wasps, though in the examples actually known at present its importance is at the most small. For with the hatching of the young bees from the cells the last duties of their mother as the guardian of the nest have been performed. The solitary bee, having now done with the building of the nest and watching of the cells, «is fully justified», as Fabre imaginatively expresses it, «in saying of itself that it has worked well during its lifetime. It has expended its life for its future family without reserve... and now it dies contentedly, since everything in its dear home is in order» (*Chalicodoma pyrenaica* Lep.). After what it has done there is no reason why it should leave this «home», and if nothing prevents it, it mostly finds its tomb in the nest. Here under the debris of the abandoned cells its remains are sometimes to be found, the last vestige of the formed «impulse to live».

With the death ot the builder the continuity of its philoprogenitive actions is interrupted. We may now turn to the description of its individualistic actions performed mainly or exclusively during the two early periods in the life of the solitary bee — its infancy and youth.

## IV. **Individualistic acts.**

### The Period of Infancy.—Life in the Cell.

The incubation period or egg-stage lasts in solitary bees for about four days, though sometimes (as in *Andrena ovina* Kl., *Anthophora acervorum* L.) it may extend for as long as three or five weeks (*Colletes cunicularius* L.). When the larva hatches, the egg-shell splits symmetrically along two longitudinal lines where the spiracles of the larva are located and along a transverse one in the region of the head. By degrees the very thin and delicate membrane (chorion), which has been broken in this way, is moved backwards, becoming folded on itself, and the shining body of the larva as yet not quite distinctly divided into segments, appears from beneath it. The shell is not, however, thrown off in those places where the egg is fastened to the provisions. Hence the hatching of the larva, if the egg were deposited sideways and not symmetrically as it always is, would meet with unsurmountable difficulties, at least when the provisions were not sticky enough.

Having thrown off the shell the larva as a rule remains where the egg was deposited, i. e., attached to the provisions whatever way the egg was. But in the case where the egg lies freely, without attachment to the convex surface of the «ball» or «lump» of provisions, the young larva at even the slightest bending or unbending of its body or at its first attempt at feeding, drops to the floor of the cell where it lies at the lowest point beneath the provisions (*Systropha*, *Rhophites*, *Dasypoda*). When the egg is fastened by one end to the wall of the cell (*Colletes*), the larva first leans out from the wall till it comes into contact with the meniscus of the provisions, into which it then transfers itself almost imperceptibly (apparently passively). Only in the genus *Ceratina* (*Ceratina callosa* F.) there is an undoubtedly active translocation of the larva from the place where the egg was fastened partly to the wall of the cell and partly to the provisions; the move-

ment is very slow and amounts only to the length of the egg. According to Brauns (1900), however, the larvae of *Allodape* have foot-like organs which enable them to grip their food. Later Friese (1914), after examination of spirit-material, describes these «pseudopodia» as short protuberances of the body-wall, sometimes hemispherical, sometimes narrower and therefore having an extraordinary resemblance to true legs. Strand (1914), who studied different material, also preserved in spirits, failed to find these protuberances and was unable to distinguish the larvae of *Allodape* from those of *Ceratina* which had been preserved with them. The question of power and range of movement in the larvae of *Allodape* requires, therefore, reconsideration.

We may note for comparison that recently hatched larvae of certain parasites and lodgers (e. g. *Sapyga, Gasteruption, Chrysis)* are capable of energetic movement, sometimes not only within the limits of one cell but extending to several neighbouring ones (the larvae of the beetles *Trichodes* and *Meloė* and also of the ensign-fly, *Gasteruption)*. Even the larvae of cuckoo-bees are at first able to move energetically about inside the cell (*Melecta armata* Pz.). Thus the larvae of the solitary bees and wasps, which find themselves in a chamber isolated from the outer world and containing an abundant store of provisions, are in a position in many respects recalling that of an endoparasite, more especially one which lives within the body of another insect larva. Hence the numerous features which they have in common: — the absence of organs of locomotion, underdeveloped sense-organs (no eyes, rudiments of antennae), delicate and colourless integument which is almost entirely lacking in hairs, bristles, etc. [1].

Finding themselves in one way or another on the provisions the very young larvae of the solitary bees assume one of the following two positions: either their ventral surface is opposed to the provisions, or they lie on their side on the provisions with their ventral surface bent into an arc or a circle. In the first case the larvae may be called «sitting» in the second «lying». The latter term must also be applied to those larvae which drop on to the floor of the cell under the provisions (see above) since they lie with their ventral surface convex and

[1] The body of the larvae of *Megachile bombycina* Rad. and some other species of *Megachilinae* is covered with short, sparse, upright hairs.

touch the provisions with one side. As a general rule the «sitting» posture may be said to occur when the provisions are more or less solid and dough- or pollen-like (*Andrena, Halictus, Melitta, Ceratina, Osmia,* fig. 43, etc.), while the lying position is adopted when the provisions are liquid, honey-like, or with a skin-like crust *Colletes, Anthophora, Macrocera).* There are, however, certain exceptions to this rule. Thus the larvae of *Prosopis, Anthidium florentinum* F., *Megachile rotundata* F., *Trachusa byssina* Pz. «sit» (on their ventral side) on the honey-like provisions (pl. X, fig. 50); similarly the larva of *Andrena ovina* Kl. does not alter its sitting posture although the provisions become extremely liquid towards the time of feeding. On the other hand the larvae (*Systropha,* etc.), which drop off their solid provisions, assume nevertheless the «lying» position.

Having thrown off the egg-shell, gathered strength and assumed the proper position, the larva begins to take food about 24 hours after its emergence. This process continues day and night and is interrupted only in case of some disturbance (concussion, contact, etc.) and during moulting. The larva, fastened to the provisions or floating on the surface, takes food only from the side of the provisions with which it is in contact, so that when the consistency is sufficiently thick, a more or less deep and wide hollow is formed (*Andrena bimaculata* K., *Halictus major* Nyl., *Osmia tridentata* Duf. et Perr., etc.). *Ceratina callosa* F. does not, however, begin to eat the «cake» at the end which it can reach directly but, as has been mentioned, changes its position and then begins consuming it just at the opposite end. Owing to this method the provisions remain attached to the wall of the cell by a narrow projection until almost the end of the larval feeding period. The larvae *Systropha, Rhophites, Dasypoda* after hatching drop, as mentioned, to the floor of the cell and bend their unusually elongate body round the base of the moulded provisions, which they manage to eat rather uniformly all round by doubling their body on itself. In this again, as in the preceding method of feeding, we cannot fail to see the tendency to isolate the provisions from the hygroscopic walls of the cell, — continuing what had been accomplished with such skill by the mother-bee.

The larva of *Xylocopa* (*X. valga* Gerst.) after eating part of the large food-mass beneath it, drops on to the side of the cell and, bend-

ing its body round the rest of the provisions, consumes them while actually supporting them. Such a change from a sitting to a recumbent posture is observed in all «sitting» larvae with the exception that the larva often does not support the provisions but finishes eating them in the place where it was laid (*Prosopis, Megachile, Osmia tridentata* Duf. et Perr., etc.). Further in *Prosopis* (*P. punctatissima* Sm., etc.), this change in posture occurs at an early stage, not the semimature larva as usual.

According to the energy of the larva, the quantity and quality of the food, the feeding continues for two (*Andrena ovina* Kl.), three (*Xylocopa valga* Gerst.) or up to four weeks [1]. Thick or hardened provisions are on the whole eaten up more slowly than thinner, more juicy ones. At any rate the whole store of provisions is eaten up entirely, apart from cases of accidental retardation in feeding [2].

Living without means of egress in a small space shut in on all sides, the larvae of bees and of the majority of wasps are placed in conditions where the food and the products of its digestion would seem liable to confusion. Provision against this is made in different ways. In the majority of bee-larvae, as in most other legless hymenopterous larvae, no communication takes place between the mid and hind intestine before the feeding is completed, the remains of digestion being retained in the intestine, so that there is no possibility of contamination of the store of provisions. This is the physiological way of separating the provisions from the excrement. Those solitary bee-larvae, which avail themselves of it, usually glue the excrement thrown out after the feeding is completed to the walls of the posterior part of the cell (*Andrena, Halictus, Melitta, Metiturga, Panurginus, Systropha*) or even simply throw it aside (*Dasypoda*). In the remaining species the excrement already begins to be excreted during the feeding process; either in the middle of it (*Megachile, Xylocopa, Ceratina* [3]) or much later, at its very end (*Prosopis, Colletes*). Howe-

[1] Friese report that the larvae of *Colletes* after eating part of the provisions hibernate, and in the spring eat the remainder. This report is, however, open to some doubt.

[2] According to Nielsen, *Colletes daviesianus* Sm. does not eat up the whole store of provisions.

[3] Also *Gasteruption caudatum* Szepl.

ver in one way or another the confusion of the food with the excreta is prevented.

In the larvae of *Ceratina* (*C. callosa* F., etc.) this end is usually attained in an original way. Owing to the circumstance that the anterior end of the larva is directed towards the top of the cell and the posterior downwards, the excrement drops to the bottom of the cell and is thus separated from the provisions which, as we have stated, are fastened to the side wall, somewhat higher up. This method, in distinction from the preceding one, may be called mechanical. It must not, however, be forgotten that primarily it is the result of the sanitary care of the mother who, contrary to the usual habit of solitary bees, deposits the egg beneath the provisions which are purposely fastened above the bottom of the cell. A method essentially the same is employed by the larvae of certain species of *Osmia* (*O. rufa* L., *O. tricornis* Latr.), and of the lodger-bees related to them, which nest in upward sloping cavities, the reeds of thatched roofs for instance. The excrement of their larvae, like that of the larvae of *Ceratina,* rolls down by the force of gravity, only this time not towards the bottom of the cell which here is elevated, but towards the lower lying entrance of the cell, i. e. in this case also directly away from the store of provisions. Moreover owing to the circumstance that the provisions are near the inner end of the cell and that the larva at this period of its development has its head directed towards the provisions and its tail away from them, the excrement of the feeding larva fall into the corner opposite to that occupied by the provisions. In every thing concerning the choice of a site for the nest, the preparation of the provisions and deposition of the egg these bees act in a manner directly opposite to that of *Ceratina* but just because of this the ends of both are attained in a similar mechanical way. Here too may be mentioned the species in which the larva supports the rest of the provisions upon its own body and so isolates them from the refuse lying on the floor, and finally those in which the excrement owing to its physical properties sticks o the walls or to other particles whenever they come in contact (*Sapyga*).

The third method is based upon what may be called the sanitary instinct of the larvae themselves which fasten each lump of excremen

to the ceiling or the upper part of the cell. This is the habit in the first place in the species of *Osmia* which live under the same conditions as the European *Ceratina* (in stems) but unlike them depositing their eggs on the provisions (*Osmia parvula* Duf. et Perr., etc.). Their parasites, the larvae of *Stelis*, behave in the same way. This method must therefore be regarded as instinctive. It must be supposed that the same method is used by the larvae of *Colletes* (*C. cunicularius* L.) which begin to void their excrement towards the very end of feeding and progressively line the whole inside of the cell with it, forming in this way something like a cocoon (pseudo-cocoon). Here too must be referred the behaviour of *Anthidium diadema* Latr., described by Fabre. By the movements of ist posterior end the halfgrown larva pushes the lumps of excrement toward the periphery of the cell fixing them there with a few silky threads. Repeated experiment has shown that the swallowing of provisions purposely soiled by an admixture of excrement is followed by langour and sooner or later (for instance before pupation) by death in the larvae of *Ceratina callosa* F.

As already mentioned, the larvae moults during the time of feeding. To follow the consecutive moults is very difficult, since the cast off skin is exceptionally delicate and in almost everything is similar to the new one and therefore not directly visible even with the aid of the microscope. Only when the larvae of *Osmia rufa* were purposely sprinkled with the pollen, which was then removed with the skin at moulting, was it possible to ascertain that these larvae moult four times during their whole life. In the larvae which are in any way fixed and apparently also in those which float on the provisions, the skin is not completely thrown off but remains attached to the body of the larva on the areas of contact with the foor or cell. Thus in «sitting» larvae the cast off skins accumulate under their anal ring. Moreover, when the growing larva rests with its posterior end on the ceiling or floor of the cell the moulted skins adhere also to these places. Later on, completing their feeding up, the larvae eat their moulted skins also.

Having finished feeding and attained full growth the larvae of many bees turn to the preparation of their cocoon, a structure observed in a variety of bees, living under so various conditions that the

real reason for it is obscure [1]. Among the solitary bees the members of the subfamily *Megachilinae* are particularly famous for their skill in surrounding themselves with a cocoon — all of them being gifted with this power. Besides these cocoons are made by the larvae of *Melitta, Macropis, Eucera, Tetralonia, Systropha* and *Rhophites* among our digger-bees, and *Euglossa, Centris, Exomalopsis, Emphor, Melissodes, Melitoma* among the exotic bees. Moreover cocoons are met with in all social bees, part of the cuckoo-bees and the majority of wasps.

As though to show that, though buried in the ground and even in direct contact with the substratum, the larvae of the bees have no reason to fear humidity, those of *Dasypoda* make no cocoon. On the other hand, the larva of *Chalicodoma* — which would seem to be excellently protected in its cell of masonry — nevertheless weaves a cocoon [2].

The building material of the true cocoon is in the first place threads and thin films secreted by the spinning glands of the larva and further its excrement and various particles either of accidental origin or purposely separated by the larvae from the walls of the cell. The excrement sometimes forming part of the actual web of the cocoon, sometimes disposed more or less regularly on its surface, forms in *Anthidium* a sort of crown on the anterior end of the cocoon.

As regards shape, the cocoons ot bees, are usually wall-cocoons, i. e. closely lining the cavity of the cell. Less frequent are the «semi-cocoons» consisting of a transverse or slanting wall which separates the part of the cell occupied by the larva from the other unoccupied part or from the exterior. They are particularly characteristic of the social wasps (*Vespidae*) and partly of the solitary ones (*Eumenidae*), but also occur in the bees (*Osmia adunca* Latr.). Only exceptionally

[1] It is known that the cocoon of the larva serves chiefly as a protection from variations in humidity and secondly mechanical influences and to some extent small enemies.

[2] Nielsen (1902) points out that the larva of one species of cuckoo-bee (*Coelioxys conica* L.) sometimes make a cocoon and sometimes manages without one, according as a cocoon is or is not made by the larva of the host (*Megachile* and *Anthophora*). This generalisation is however not always justified. Thus I found cocoons of *Coelioxys rufescens* Lep. in the cells of *Anthophora furcata* Pz. Besides, the larvae of some parasites always make a cocoon, though one is not made by the host-larvae (*Ceratina callosa* F., *C. dupla* Say).

in the bees (though usually in the digger-wasps) free cocoons which have a shape of their own altogether independent of that of the cell, are found; they are attached to the walls only by means of special weak threads (*Osmia rufa* L. [1]). The larvae of the majority of bees, however, make no cocoon.

Having finished the tidying up of the cell and if necessary made a cocoon, the larvae assume a more or less straight (*Prosopis, Colletes, Andrena, Panurginus, Megachile*, etc.), or bent (*Anthophora*) position, or even with their head and tail touching (*Macrocera*), but not always with their anterior end directed towards the cell-cover (*Xylocopa*); some of them also firmly attach the posterior half of their back to the bottom of the cell or to the corresponding part of the cocoon (*Anthophora pubescens* F., *Tetralonia malvae* Rossi).

At last having assumed the proper position the larva lapses into a state of rest (the larval resting stage). This quiescence is usually very deep; the larva executes no discernible movements, shows no reaction when stung and therefore appears as if dead. In some of them however, the torpor is less profound and at the slightest irritation they begin to move energetically; they bend, unbend and turn round on their longitudinal axis. The larvae of *Osmia tridentata* Duf. et Perr. even produce a peculiar sound by rubbing their backs against the elastic wall of the cocoon.

The resting stage continues for a varying space of time from two or three weeks (*Osmia rufa* L., *Andrena bimaculata* K.) to several months, including the winter (*Prosopis, Colletes, Melitta*, etc.). It is remarkable that event among larvae of the same species a great variation is often observed in this respect; part of them (apparently the majority) after passing through the resting stage undergo further development, while the remainder continue in a stage of torpor lasting in this instance for about a year. Such a partial check in the development (partial diapause) has been observed in *Colletes cunicularius* L. (the author).

But now comes the time of awakening. If the larva was previously bent or glued to one place, it now loosens itself and straightens

[1] In the wasps double cocoons sometimes occur; these represent a combination of the wall — and free — cocoon, the latter being enclosed in the former.

out. Then a week later follows the transformation into a semi-pupa a short transitory stage where under the larval skin the pupal characters are already present and partly visible on the exterior. Finally the last larval skin is thrown off and the pupa lies in the cell with the adult shape and all the mature insect's appendages, even those of the mouth, all lying freely, as if for show, folded on the ventral side (pupa libera); only the wings on the sides of the thorax stand out by contrast as mere rudiments. On the dorsal side of the edges of the abdominal segments and to some extent in other parts of the body, there may usually be seen numerous not very sharp spines; owing to the presence of these it is not so closely in contact with the walls of the cocoon or cell — an adaptation preventing unnecessary friction and so facilitating further transformation.

The pupal stage is not usually of long duration: only about a month and only rarely protracted so long as to include the winter (*Eriades florisomnis* L. and apparently *Osmia coerulescens* L.) [1]. Gradually under the transparent skin of the pupa pigment begins to appear: this is the skin of the adult insect beginning to colour. Finally the last moult takes place, and at the same time the transformation into the adult stage, the winged bee.

It might be expected that the developed bee would only remain a few days now to gather strength in order to get free. Some of them indeed do act in this way, as for instance, *Halictus, Ceratina, Xylocopa*, and some species of *Osmia*, etc. The majority however, again relapse into a state of repose, not infrequently continuing for months. In this way many of the solitary bees pass the winter.

Thus the whole period of infancy of the bee — from its birth almost till sexual maturity — is spent in one place, the cell. In this respect the bees alone of all organisms living on the surface of the ground (apart from the wasps and some beetles) rather remind one of the higher vertebrates, such as a few mammalia and birds, which bring up their young ones in nests. In both cases this remarkable quiescence of the young generation is established at the price of intense parental care, usually entailing considerable locomotion. Thus *Chalicodoma muraria*, according to Fabre, must cover up to

[1] Once in my experience a pupa of *Ceratina callosa* F. hibernated, but this is abnormal in the genus.

400 Km. in flight; but as a result its fifteen descendants are able to develop on the spot without further trouble.

## V. The period of Youth.

However long or short may be the time during which the developing bee sleeps in the cell, at last it awakens, if no accident has prevented it, and endeavourts to get out. It is difficult to tell what the direct cause of this awakening may be, but one thing is certain: the bee wants better conditions for breathing than those which have surrounded it until now.

As to the direction chosen by the bee for leaving the cell, the investigation of Fabre on *Osmia tridentata* Duf. et Perr. and some other species, have shown that two factors are involved; the force of gravity and the action of the atmosphere, as for instance the influence of fresh air. Under natural conditions these two factors usually reinforce each other, compelling the bees to make their way upwards, where the exit-hole of the nest is to be found. Fabre created various artificial combinations of these conditions. In one frequently repeated experiment he placed the tubes with the cocoons in a horizontal position and so eliminated the influence of gravity; both ends of the tubes were open and consequently exposed to the same atmospheric influence. The result was as follows: of ten *Osmia*, which bit their way through the corresponding number of cocoons, the five on the left moved out by the left hand opening and the five on the right by the right hand one, to do which some of them were obliged to turn round, i. e. to change their primitive orientation. But when one end of the horizontal tube was tightly shut, all the *Osmia* made their way to the open end and this time the remarkable symmetry in behaviour was not observed. In both cases moreover there was evidently a tendency to reach the open with the least expenditure of energy. From this and similar experiments the investigator drew the conclusion that *Osmia* and some other bees «perceive the open air».

Under normal conditions the awakened bee does not require to alter its direction, since the adult larva must be supposed to possess

the same «sense of free air», and therefore before sinking into torpor it lies down with its head directed towards the outlet. But the larva of *Xylocopa* (*X. violacea* L., *X. valga* Gerst.) having finished feeding turn usually with their anterior end towards the bottom of the cell and change into pupae in this position. Later, on the adult stage, they turn again with their head towards the cell-cover [1].

Thus it is only necessary for the awakened bee to set about destroying either a particular wall of the cocoon (if one exists) or the wall of the cell directly. Usually the front wall (cell-cover, transverse partition) is broken through, but in some cases, which will be described later on, it is the anterior part of the lateral wall. If the wall to be destroyed (and it is at least a specially constructed one) is too hard, the young bees moisten it with their saliva (*Anthophora fulvitarsis* Brullé, *A. acervorum* L., *Osmia rufa* L.). This fluid is used very economically, being exuded from time to time in small drops on the particularly hard parts of the wall which is thus softened; the rest is done by the mandibles and feet. Having made a considerable breach the bee repeatedly tries to get out through it, and continues till it meets with success.

In independent nests (anodalous) it is usually sufficient for leaving the cell to perform this work once only, viz. to breack through the cell-wall, though that may be made thicker by the nest-cover. It is remarkable that *Chalicodoma muraria* L., as the experiments of Duhamel and Fabre have shown, is not able to overcome two obstacles (the natural cover of the nest and a paper cap) separated by an empty space, though it can gnaw through them when they are tightly joined. The impediment is therefore of a psychological rather than of a mechanical nature. Once the insect has come out of its stony dwelling, it has done everything that its normal destiny required for its liberation. When able to crawl on the cover of the nest, its labour is over, it has finished tunnelling and is free. To undertake once more the work it should have had to do only once during its lifetime, is beyond the insect's powers, for the very simple reason that the impulse is

[1] Reaumur reports that *Xylocopa violacea* L., besides a lateral outlet, makes of the opposite end of the nest a second, facilitating the exit of the developed bees. This report has however received no confirmation.

wanting and «the mason-bee perishes for want of the slightest glimmer of reason». (Fabre.)

In leaving branched nests bees behave much as in the preceding case (leaving an independent nest), the adult bee making its way out without disturbing the inhabitants of the neigbouring cells. Indeed, as direct acquaintance with the old galleries of deserted branched nests and with their gypsum casts shows, these deserted galleries retain the construction generally characteristic of the respective species of bee (*Andrena ovina* Klug, *Anthophora fulvitarsis* Brullé, *Tetralonia malvae* Rossi, *Panurginus,* etc.). Here the bee does not reach the surface of the substratum by a separate tunnel from each cell, but, having made its way through the lateral gallery, gets into the main one, which leads to the exterior. Thus the bee gains the open air by the same path as that used by the mother bee when she was building them. In both instances a great economy of effort is evidently obtained, since the main gallery is common to all the cells of the nest.

As to linear nests, the emergence of the young generation presents one specific disadvantage: the older the individual, the nearer the moment for it to leave the nest, the further it will find itself from the outlet, to which the youngest is, on the contrary, the nearest. This violation of the right of «primogeniture», which demands that the order of leaving must become the reverse of that of birth, is the direct consequence of the method applied in building typical linear construction. The division of the nest gallery into a series of cells begins at the bottom and is continued in the direction of the outlet; therefore the cell last constructed is also the uppermost, or one nearest the exit.

Hence it is obvious that the greather the number of cells in a gallery, the longer their building takes; and the more rapidly the metamorphosis proceeds, the more significant is the different in the ages of individuals developing at the opposite ends of the gallery and the greater, therefore, will be the effect of this specific disadvantage. Thus in the lower cells of *Ceratina callosa* F., fully developed bees not infrequently occur when the upper cells are still occupied by young feedding larvae, and sometimes apparently even by eggs. Usually, however, the difference is not so considerable. At any rate the necessity of contending against the specific disadvantage of linear nests exists and is met in various ways. To begin with the lodger-

bees, the typical builders of linear nests, often displaid the tendency to divide up their egg-laying into a number of separate series consisting of a small number of cells each (for instance *Osmia tricornis* Latr., according to Fabre), thus facilitating the escape of the bees in the future.

Then, as we know, these bees have the characteristic habit of placing the male cells nearer the exit than the female ones. Owing to such a «proterothesis of the males» the latter, developing more quickly than the females, are able to clear the way for their passage out of the nest. Further the individuals which are the first to develop may make outlets into the adjoining cells and then patiently wait for the maturity of their neighbours, which are blocking the way in front of them, before escaping (*Ceratina cucurbitina* Rossi, according to Duf. et Perr.).

But if waiting proves futile (the cell standing in the way, perhaps, containing only dried up provisions, etc.), or if the bee wanting to get out loses patience, it tries to slip itself between the all wof the canal and the developing individual or cocoon, blocking the passage. Usually the attempt is successful in sufficiently wide galleries, at any rate it is made carefully so that the individuals in the cells passed through scarcely suffer, if at all. In other instances, sometimes even without apparent necessity, bees will bite through their own cocoon and cell at one side and come out each by a separate passage (*Osmia tridentata* Duf. et Perr., especially in the case described by Verhoeff). This method is, however, much more frequently employed by the cuckoo-bees and by various parasites than by their hosts.

These difficulties in leaving the nest are moreover essentially relieved by the intercalation in the life-cycle of a «resting bee» stage (see above), particularly when this stage continues for a long time, months for instance, as with *Osmia rufa*. Here the difference of two or three weeks in the ages of the individuals in a nest loses its significance.

I have been able to demonstrate in *Ceratina callosa* F. the existence of a peculiar contrivance for leaving the nest. The essence of this plan is that the nest gallery is very wide and the inhabited cells are separated from each other by empty spaces — cavities with of double or triple partitions (fig. 69). So here there is plenty of room both in the transverse and longitudinal directions. The former enables the indi-

viduals making their way towards the outlet to pass those still developing and the latter ensures sufficient room at suitable intervals to receive rubbish derived from the destruction of the transverse walls. It has been shown by experiment that if a larva or pupa is placed in each of the double partitioned cavities, the winged *Ceratina* at the bottom of the nest are unable to get out and in their attempts to do so they maim the others [1].

Having in one or the other way gained its freedom, the young bee breathes deeply and soon excretes the meconium. *Osmia rufa* L., and *Anthophora acervorum* L., having first risen into the air above the nest, turn their head towards it, flying at a distance of a few centimetres through several circles, thus committing to memory the appearance of their birthplace. It must be supposed also that other bees living in colonies behave in the same manner, so that the colony may be perpetrated in one place. As already mentioned, certain solitary bees on leaving the nest meet with their mothers (*Halictus quadricinctus* F., *Ceratina callosa* F., *Xylocopa valga* Gerst., etc.), but they do not work in common.

The time when many (apparently the majority) of solitary bees gain their liberty and make their first appearance coincides with the blossoming of certain flowers. In some cases these are the same flowers from which latter on they gather their provisions (*Tetralonia malvae* Rossi, *Andrena florea* F., etc.). At times the bees may appear considerably earlier than the blossoming of their favourite flowers so that at first they seek some other, though usually some particular plant, — *Anthophora acervorum* L., on *Corydalis solida, Osmia rufa* L., *Gagea; O. tricornis* Latr., on the almond. Finally in a few bees the time of appearance is extended and appears to be unconnected with the flowering of particular plants (*Ceratina callosa* F., *Xylocopa valga* Gerst., pl. VII, fig. 29, etc.).

The leaving of the nest and the visiting of flowers usually takes place at certain hours of the day. In this respect almost all the bees,

[1] Spinola (1808) in *Ceratina cucurbitina* Rossi *(albilabris* F.), as well as Dufour in *Odynerus rubicula* Duf., state that here not only the leaving of the nest but even the development to maturity proceed in an order just the reverse of that of the building of the cells; but these cases are very doubtful (Malyshev, 1913, p. 4).

as well as wasps, are diurnal animals, flying from sunrise till sunset, and at more or less definite hours. They favour especially the hours of the morning from the moment when the sun has given sufficient warmth till about noon. There is then an interval, though not a universally respected one, till about three o'clock. Towards evening flying again increases and ceases usually an hour or two before sunset (Friese). Generally speaking the flying time of diurnal bees corresponds to the curve of secretion of the nectar in diurnal plants. Such variations in the frequency of flight are not however characteristic of certain bees (*Anthophora acervorum* L., for instance), since in fair weather they are quite often seen from morning till sunset, being in this respect inferior only to the honey-bee, humble-bee and certain wasps (*Vespa crabro* L.), which sometimes return home long after the sun has set. The humble-bees are moreover known to fly in the far North during all the 24 hrs. and in the South to visit the flowers of the acacia during warm moonlit nights. Further there is an indication (Schrottky) that the bee *Ptiloglossa ducalis* Sm. living in Argentina flies in preference at dawn and dusk and is therefore a crepuscular insect. *Megalopta*, however, seems to fly only by night. Sometimes it comes flying into a room towards the light of a lamp, laden with pollen and is thus a true night-bee. *Xylocopa tranquebarica* F. flies by night also [1].

Having left the nest where born, solitary bees are in need of a temporary lodging for rest or for shelter in foul weather. Such shelter may be provided by the maternal nest, where the young bees return at nights. But not infrequently they take refuge in the corollae of flowers or simply upon branches of trees or in places where they do not build nests for themselves, for instance between the thatch of roofs, and the like.

Solitary bees as a rule both begin and finish their work in the same spring or summer that they left the nest. Sometimes however it has been observed, at least in Europe, that *Halictus*, *Ceratina* and *Xylocopa*, after leaving the cells, hibernate and only begin to work the next spring. In this case, therefore, the question of a shelter for the winter arises. This, as far as it is possible to ascertain, is generally

[1] According to H. von Ihering (1904) a nocturnal mode of life is led also by the social wasp known in Brazil as *Apoica;* this wasp posesses strongly convex simple eyes like *Megalopta*.

the old parental nest (*Halictus cylindricus* F., according to Fabre; *Xylocopa frontalis* Oliv. according to Bertoni and Scrottky; *Ceratina callosa* F., according to the author).

Sometimes, however the old nests of other species, which build in quite different conditions are chosen for hibernating. Thus *Xylocopa violacea* L. hibernates in the earth in the abandoned nests of *Anthophora*. Finally in some instances a special shelter for the winter — a burrow under a stone, is prepared, e. g. in *Halictus morio* F., according to Verhoeff[1].

Sometimes on bright days in October and November the hibernating bees leave their shelter to bask in the sun and to indulge in honey, if occasion permits it (*Ceratina*, according to Friese). At any rate the winter is spent by all of them in a state of torpor. The only exception to this is the honey-bee (*Apis mellifera* L.) whose associations are organized to form, one may say, a single individual, capable by varied and complex activities of maintaining during the whole winther not only the constant temperature necessary for keeping the bees awake, but also an adequate supply of food for the nest.

In the wast majority of cases the work of providing for the progeny does not begin in the solitary bees until after mating. Sometimes pairing already occurs within the nest when the young bees have emerged from the cells (*Halictus cylindricus* F., *Osmia tricornis* Latr.), but more often outside it, at the threshold of the parental home or somewhere near it, on the ground, on the stems of grasses, on flowers, etc. As an exception one certain generation of *Halictus* (see farther on) does without it. But it is not impossible that pairing may sometimes take place after the beginning of work (optionally with *Ceratina callosa* F.).

The external appearance of the fecundated females alters perceptibly as time goes on, chiefly in that they become considerably bigger (*Osmia rufa* L., *Anthophora acervorum* L., etc.). This increase in size as in other insects which have reached the imaginal stage, is the result of a telescopic extension of the segments of the abdomen, there the ovaries are growing and the eggs maturing.

[1] It is recorded (Friese) that *Ceratina* also builds for the winter special galleries in plant stems like those in which they nest in summer, but it seems to me that there is no evidence to prove it.

From this moment the behaviour of the females also changes. They display greater agility and are more frequently met with on flowers and near their nests. This is the true time of flight; it includes also the time of regular work. According to the time of flight among the solitary bees one may distinguish spring, summer and autumn forms, with the subdivision of early-spring (*Andrena ovina* Kl.), late-spring (*Eriades florisomnis* L.), early-summer (*Systropha planidens* Gir.), mid-summer (*Megachile bombycina* Rad.) and late-summer forms (*Rhophites hartmanni* Fr., *Colletes daviesanus* Gm.).

As may be inferred from the preceding statements, a varying period may elapse between the appearance of a given bee and its time of flight: for some species it is only a few days (*Andrena ovina* Kl., etc.), for others it is measured by weeks (*Anthophora acervorum* L.), and there are some where it lasts for many months (in *Ceratina callosa* F., about ten). At any rate the time of flight or, what is the same thing, the beginning of work for the benefit of the young usually coincides with the blossoming (sometimes en masse) of certain flowers, from which the provisions are collected, either mainly or exclusively. This remarkable «synchronism» has attracted the attention of several authors. Thus Réaumur already considered that *Osmia papaveris* Latr. did not begin its work until after the first flowers of *Papaver rhoeas* had unfolded. The height of activity is attained when these flowers are in full bloom. Fabre further points out that the building of the nests of *Osmia tricornis* Latr. coincides with the blossoming of thyme (*Thymus serpyllum*). Again, according to Pierce (1904), the flight of *Epinomia tringulifera* Vachal synchronizes with the flowering of the sunflower (*Helianthus annuus*). Similar coincidences have several times been pointed out and by me (e. g. in *Systropha, Macropis, Rhophites, Tetralonia, Lithurgus*). But in order to obtain sufficiently complete and exact data of this kind, it is, of course, necessary that long continued observations should be made by a series of investigators.

The regular work of building the nest does not start at once —repeated preliminary attempts at working in different places are made, and the nests which are first begun are abandoned altogether. Particularly frequent attempts at building a nest in different places are observed in the digger-bees; but other bees too have the same habit.

*

Thus *Osmia caerulescens* L., after occupying a rush begins to construct a partition in it, but leaving it unfinished, starts a second one, and so on; sometimes it brings a little pollen, but lays no egg. This phenomenon is also known in the social wasps (Peckham) and in birds (Wagner). All these activities are apparently signs of an awakening maternal instinct. The hesitation of the bee does not however last for a long time; its actions soon become ordered and deliberate. The cycle of the events to be described has closed: the period of youth has ended, and the time of regular work, the adult period, is beginning.

(To be continued.)

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## Explanation of Plates III-XV.

PLATE III:

Fig. 1.—Diagram of a bilateral hillock *(Colletes cunicularius): A,* from above; *B,* in longitudinal section; *o,* entrance hole; *mkn,* anterior half; *mln,* posterior half.

Fig. 2.—A radial tumulus *(Tetralonia malvae).*

Fig. 3.—An eccentric tumulus *(Halictus sexcinctus).*

Fig. 4.—An acentric tumulus *(Anthophora bimaculata).*

Fig. 5.—An asymmetrical tumulus *(Dasypoda plumipes).*

Fig. 6.—A closed hillock *(Andrena ovina);* compare fig. 58.

PLATE IV:

Fig. 7.—Diagram of a regressively branched nest *(Colletes cunicularius): a-d,* main tunnel; *a-b,* entrance canal; *b-d,* descending section; *e,* lateral canal; I-V, cells.

Fig. 8.—A progressively branched nest *(Systropha planidens): c-d,* intermediate canal. Other lettering as in fig. 7.

Fig. 9.—A stationarily branched nest *(Andrena ovina)*.

Fig. 10.—A dispersedly branched nest *(Halictus sexcinctus)*: *h*, supplementary canal.

Fig. 11.—A linear-branched nest of the first type *(Xylocopa valga)*.

PLATE V:

Fig. 12.—Diagram of an empty cell of *Colletes cunicularius*: *a-b*, longitudinal axis; *c-d*, horizontal axis; *e-f*, perpendicular axis; *o*, centre of the cell; *p*, membranous threshold in its mouth.

Fig. 13.—Diagram of an empty cell of *Osmia rufa*: *p*, «threshold of Fabre», a half monthly partition marking the limits of the cell, which will be completed later. Compare fig. 19.

Fig. 14.—Diagram of a stored cell of *Prosopis communis*.

Fig. 15.—Diagram of a stored cell of *Colletes cunicularius*.

Fig. 16.—Diagram of a stored cell of *Tetralonia malvae*.

Fig. 17.—Diagram of a stored cell of *Anthophora acervorum*.

Fig. 18.—Diagram of a stored cell of *Melitta leporina*.

Fig. 19.—Diagram of a stored cell of *Osmia rufa*.

Fig. 20.—Diagram of a stored cell of *Panurginus labiatus*.

PLATE VI:

Fig. 21.—Diagram of a stored cell of *Andrena ovina*.

Fig. 22.—Diagram of a stored cell of *Meliturga clavicornis*.

Fig. 23.—Diagram of a stored cell of *Dasypoda plumipes*.

Fig. 24.—Diagram of a stored cell of *Systropha planidens*.

Fig. 25.—Diagram of a stored cell of *Xylocopa valga*.

Fig. 26.—Diagram of a stored cell of *Ceratina callosa*.

Fig. 27.—Diagram of a stored cell of *Lithurgus fuscipennis*: *a*, egg-chamber *b*, provisions; *c*, barricade (not a cell-cover).

Fig. 28 —Diagram of a first cell of *Bombus hortorum*.

PLATE VII:

Fig. 29.—*Xylocopa valga*, young female visiting flowers of white *Phlox*; × 1.

Fig. 30.—*Systropha planidens* with a full load of pollen grains on its abdomen; × 3.

Fig. 31.—*Dasypoda plumipes* with a full load of pollen on its hind legs; × 3.

Fig. 32.—*Melitturga clavicornis* with «muffs» of pollen paste on its hind legs; × 3.

Fig. 33.—The hind leg of *Macropis fulvipes* with a full load of pollen paste; × 7.

PLATE VIII:

Fig. 34.—A stored cell of *Prosopis communis* dissected from the front side. The surface of honey-line provisions and egg on it are seen; enlarged.

Fig. 35.—Part of cell of *Colletes cunicularius*. The egg is fastened to the ceiling of the cell; × 3.

Fig. 36.—Part of cell of *Andrena ovina* dissected from the side before the liquefaction of provisions took place; × 3.

Fig. 37.—A cell of *Andrena ovina* dissected fron above after liquefaction; × 3.

Fig. 38.—A cell of *Andrena florea* with small honey drops on the walls; × 3.

Fig. 39.—A cell of *Halictus major* and part of the main tunnel in longitudinal section; × 1,7.

PLATE IX:

Fig. 40.—A cell of *Systropha planidens* dissected from above. The spiral cell-cover is partly seen on the right side; × 3.

Fig. 41.—A cell of *Rhophites canus* dissected from above. The spiral cell-cover is visible on the left; × 5,5.

Fig. 42.—A stored cell of *Panurginus labiatus;* × 7.

Fig. 43.—The cell of *Panurginus labiatus* with a semi-adult larva and provisions; × 7.

Fig. 44.—Fully moulded provisions of *Dasypoda plumipes;* × 3.

Fig. 45.—A stored cell of *Dasypoda plumipes* seen from above; × 1.

PLATE X:

Fig. 46.—Fully-moulded provisions and egg of *Xylocopa valga*, male; × 3.

Fig. 47. –Spheroidal provisions with egg of *Systropha planidens* seen from the side; × 3.

Fig. 48.—A cell of *Bombus hortorum* with the bundles of eggs; × 3.

Fig. 49. –A cell of *Bombus fragrans;* each egg lies in the separate chamber; × 4.

Fig. 50.—A young larva of *Trachusa serratulae* «sitting» on the provisions; × 3.

Fig. 51.—A stored cell of a Scarabaeid-beetle, *Lethrus apterus;* the egg lies in a special chamber, apart from the provisions; × 2.

PLATE XI:

Fig. 52.—A stored cell of *Eriades truncorum* in longitudinal section; × 3.

Fig. 53.—A cell of *Anthidium florentinum* dissected from above; × 3.

Fig. 54.—A cell of *Osmia tridentata* dissected from the side; × 3.

Fig. 55.—A cell of *Megachile centuncularis;* × 3.

Fig. 56.—A cell of *Lithurgus fuscipennis;* × 1,7. Compare fig. 27.

Fig. 57.—A nest of *Anthidium laterale;* the first automorphous cell and bee itself are seen on the floor of a special nest-cavity; × 7.

PLATE XII:

Fig. 58.—The tumulus of *Andrena ovina* with an entrance hole always closed; × 1.

Fig. 59.—A preparation of the nest of *Andrena bimaculata;* the last lateral tunnel is filled out with gypsum; reduced.

PLATE XIII:

Fig. 60.—Two plasters of the *Tetralonia malvae*'s burrows; the arch-like tunnel before cell seen from the left; reduced.

Fig. 61.—A preparation of the stationarily branched nest of *Andrena ovina;* reduced.

Fig. 62.—A preparation of the progressively branched nest of *Systropha planides;* reduced.

Fig. 63.—A preparation of the *Rhophites hartmani*'s nest; reduced.

PLATE XIV:

Fig. 64.—A preparation of the dispersedly branched nest of *Halictus major;* slightly reduced.

Fig. 65.—A preparation of the chambered nest of *Halictus calceatus;* × 1.

Fig. 66.—A preparation of the linear-branched nest of *Trachusa serratulae;* × 1.

PLATE XV:

Fig. 67.—A composite nest of *Osmia caerulescens* built under glass in a little box; × 1.

Fig. 68.—A linear nest of *Osmia rufa* built in a bulrush tube; × 1.

Fig. 69.—A part of the nest of *Ceratina callosa;* cells separated from one another by double partitions; × 1.

Fig. 70.—A pseudo-honeycomb of *Anthidium laterale* seen from the under side; × 2,5; compare fig. 57.

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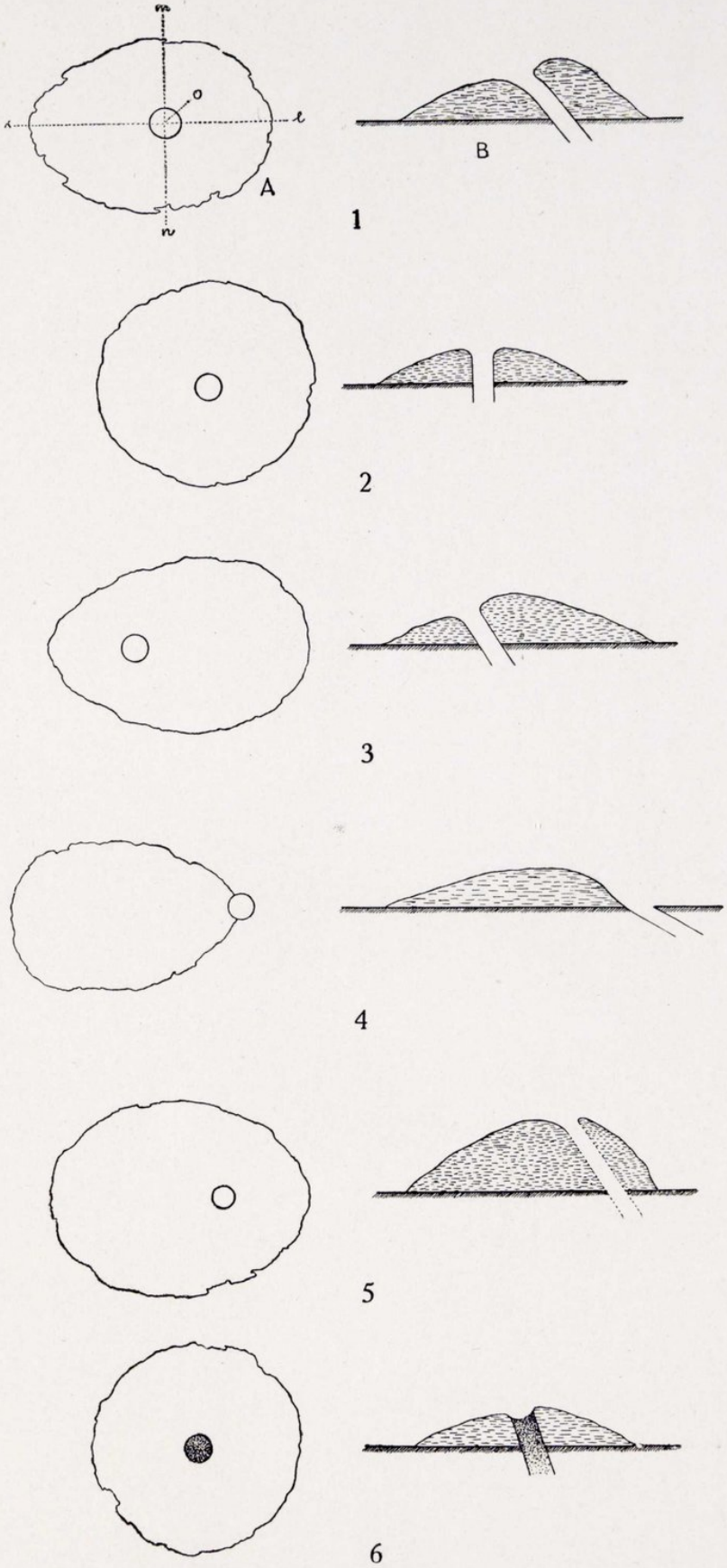


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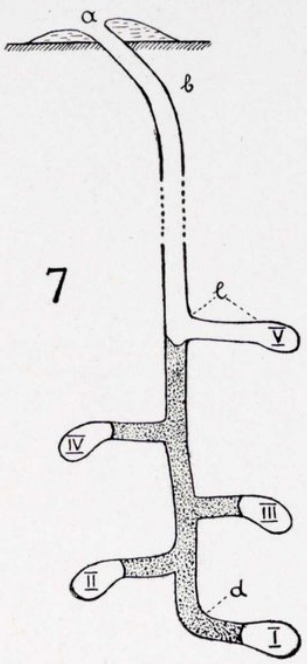


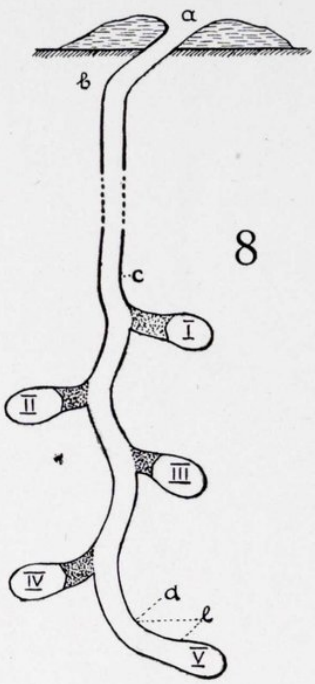


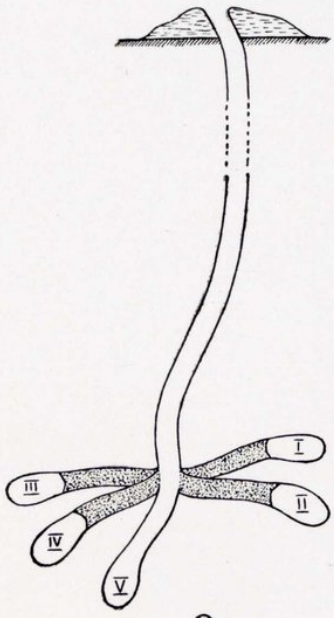


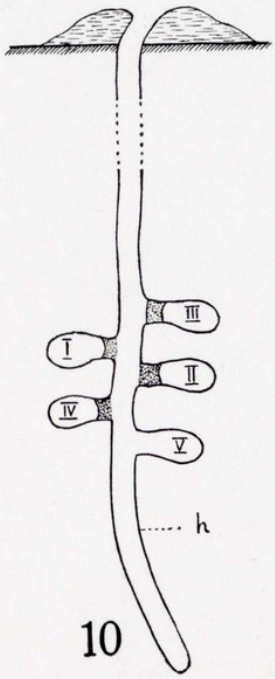


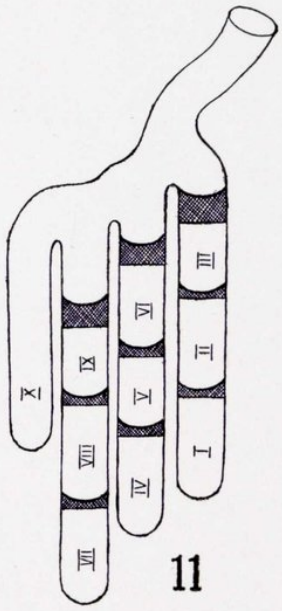


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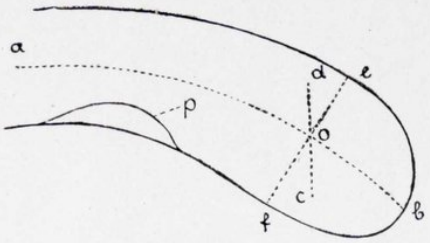


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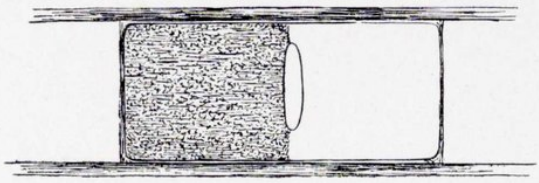

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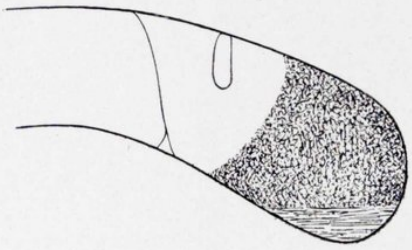

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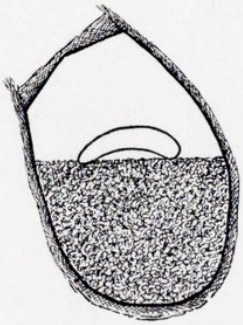

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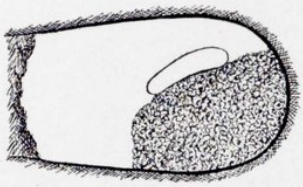

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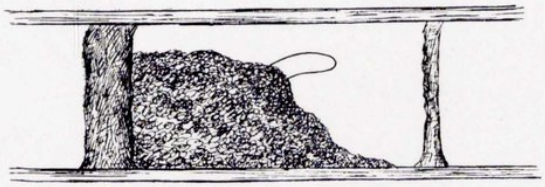

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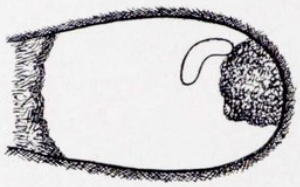

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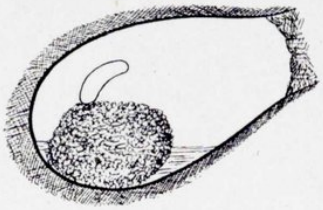

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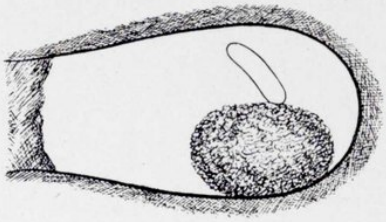

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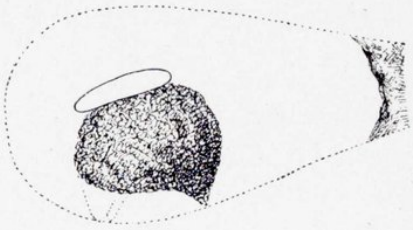

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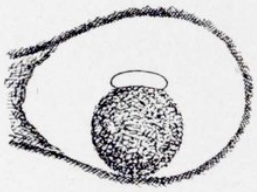

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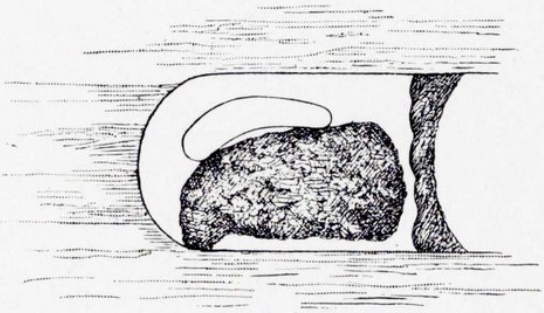

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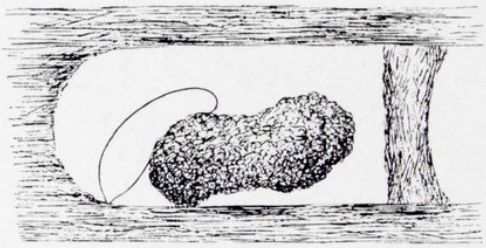

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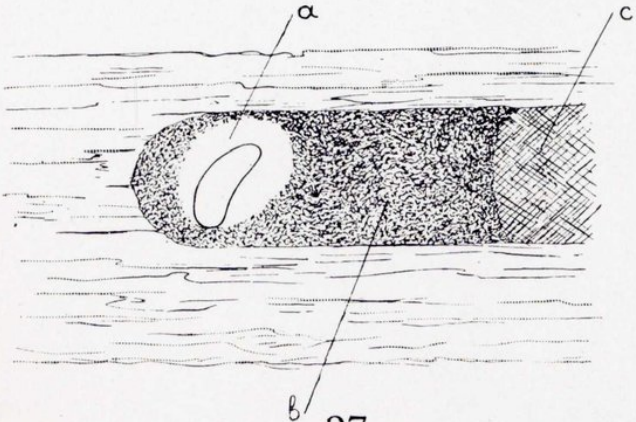


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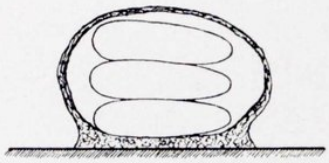

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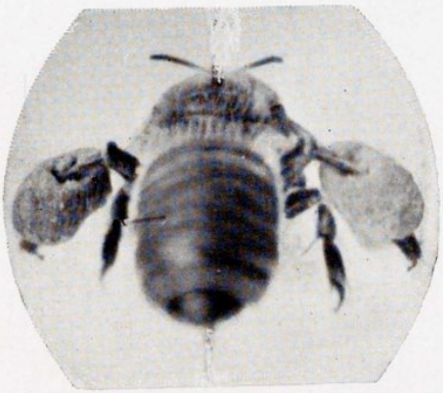

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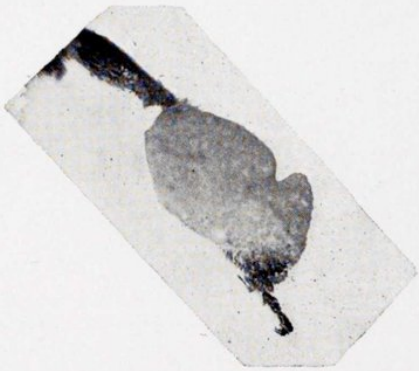

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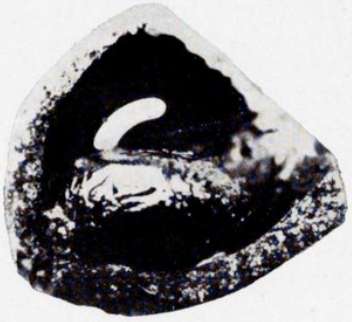

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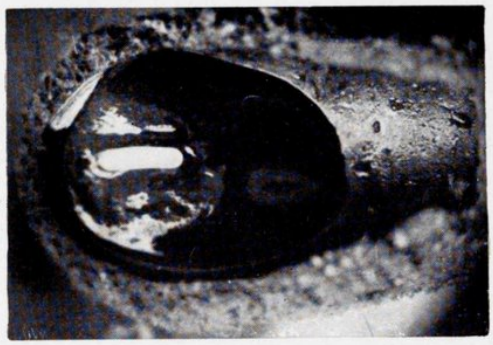

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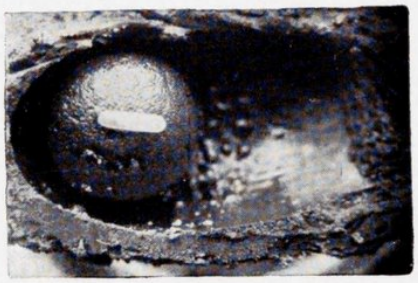

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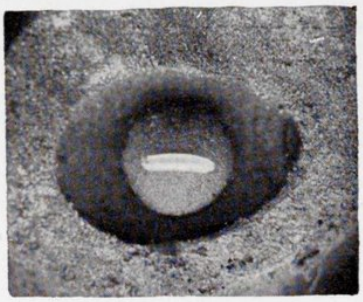

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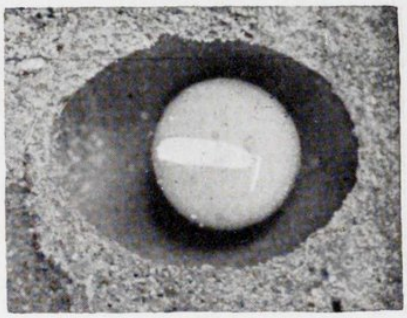

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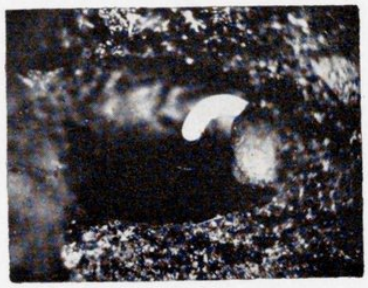

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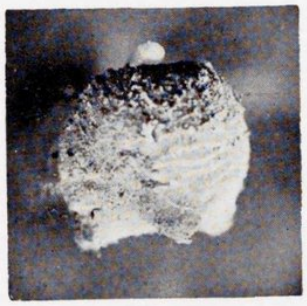

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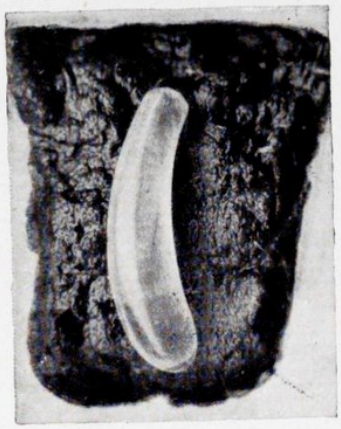

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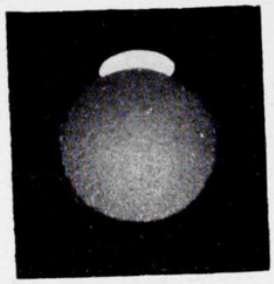

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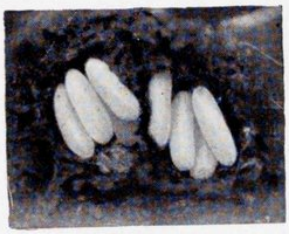

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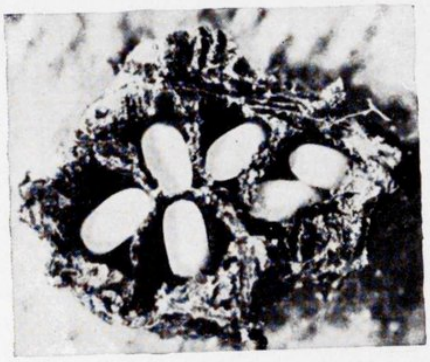

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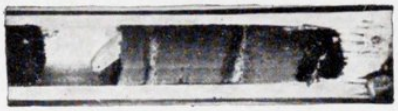

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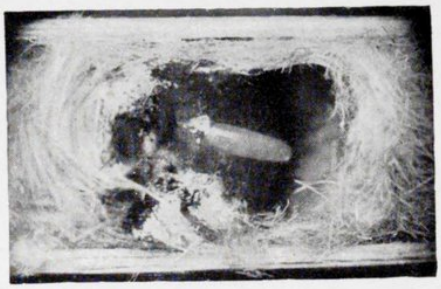

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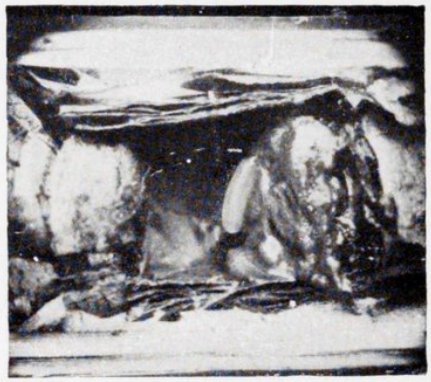

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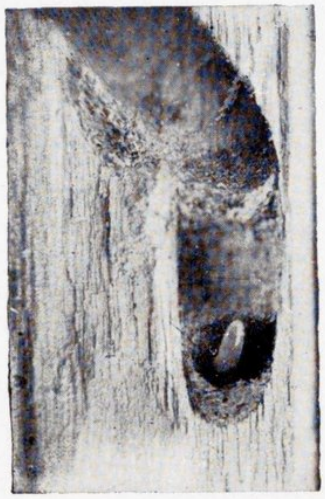

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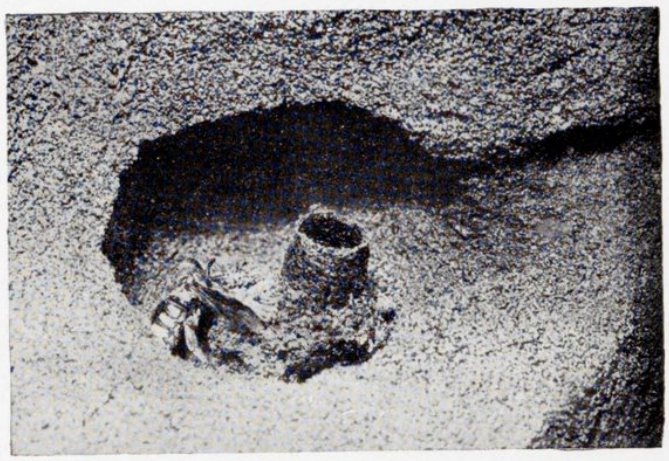

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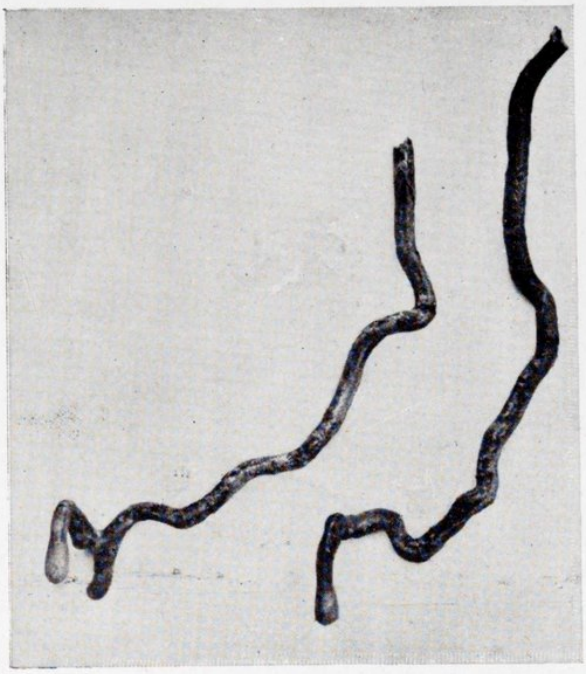

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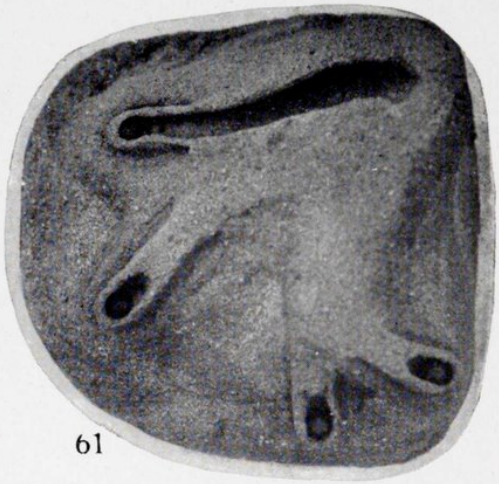

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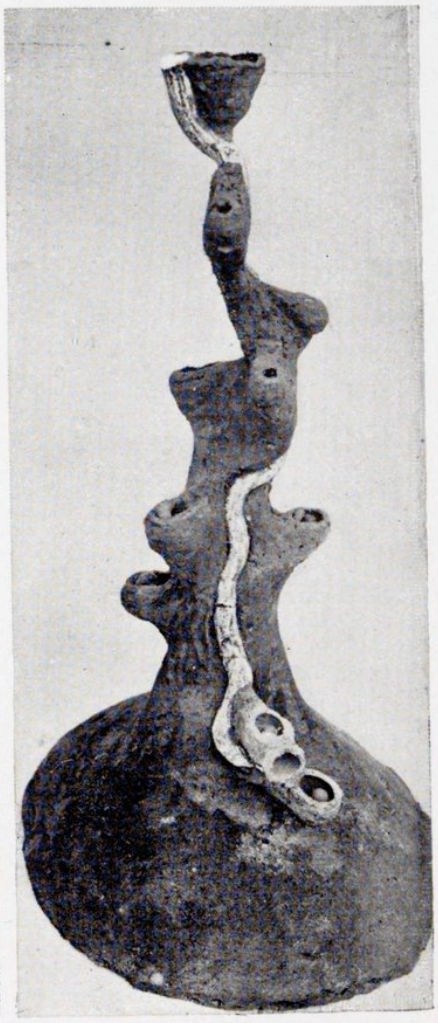

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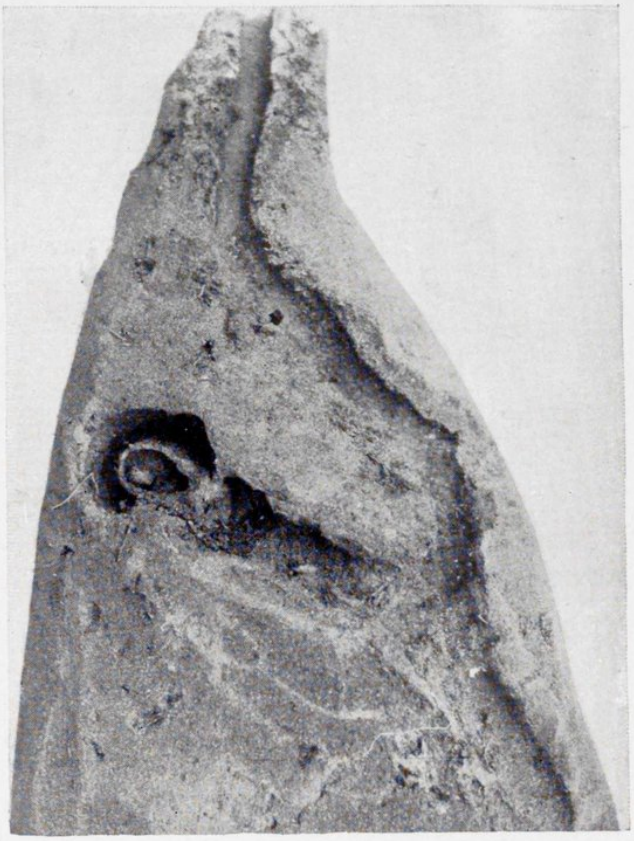

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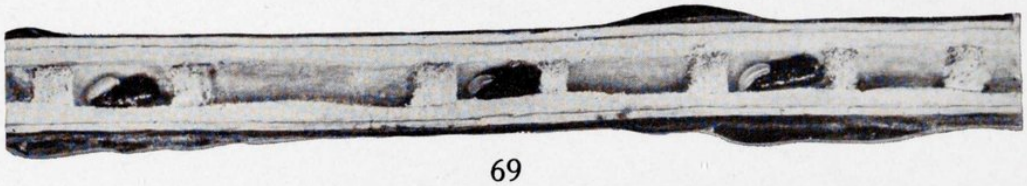

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